

BIOLOGY FOR STUDENTS OF PHARMACY

BY

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PREFACE

This book is designed to provide a course in biology for students preparing for the Preliminary Scientific Examination of the Pharmaceutical Society of Great Britain. Although primarily written with this object, the types selected include those usually dealt with in a general biology course, examples of drug interest being introduced only where they also serve as biological illustrations.

The arrangement of the chapters has been decided partly by the fact that the published syllabus is divided into plant and animal sections, and partly because it is often convenient, in a college course, to treat the two divisions separately. Sufficient cross-references are given, however, to indicate the general interdependence of living organisms, whilst the chapters on Foods and Digestion, and on Evolution and Heredity, embrace examples drawn from both plant and animal kingdoms.

Although the subject-matter has been confined to some 400 pages, care has been taken to include the fundamental principles of the science which will form a foundation for the pharmaceutical student's later work in pharmacognosy and physiology.

As, during his course, the Preliminary Scientific student will also be studying chemistry and physics, an elementary knowledge of these subjects has been assumed.

Biology is essentially a practical science, and whilst no direct instructions on laboratory work have been included, it is assumed that this will form an integral part of the course. The examples and experiments described throughout the book should form a satisfactory basis for this purpose.

The illustrations, for the most part, have been specially prepared for the book, mainly by the author, but several have been taken from various publications of Messrs. Edward Arnold & Co. They are intended not only to amplify the text, but to give the student an idea of what should be attempted in making original class records.

The author wishes to acknowledge his indebtedness to the publishers for permitting him to reproduce diagrams from Roaf's 'Textbook of Physiology' (Figs. 129, 132, 134, 135, 138, 139), de Beer's 'Growth' (Figs. 27, 39, 182), Hill's 'Manual of Human Physiology' (Figs. 141, 145, 166), Kirk's 'British Garden Flora'

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(Figs. 102, 104, 106, 107, 113), Watson's 'Elementary Botany' (Figs. 55, 93), Dallimore and Jackson's 'Handbook of the Coniferae' (Fig. 78), and Shann and Gillespie's 'School Certificate Biology' (Figs. 163, 164).

Thanks are also due to N. E. Hickin, Esq., B.Sc., who has drawn certain diagrams (Figs. 114, 115, 117, 119-121, 150, 152-159, 162, 165, 167, 169-174, 176-179, 189-192, 197, 199); to E. George, Esq., for the photomicrograph of *Dracæna* (Fig. 38); and to Messrs. Flatters and Garnett, who prepared the photomicrograph of the frogbit (Fig. 51) from a slide made by the author.

In conclusion, the author wishes to thank his colleagues in biology for helpful suggestions offered during the preparation of the book.

E. J. M.

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BIOLOGY FOR STUDENTS OF PHARMACY

CHAPTER I

INTRODUCTION. THE CHARACTERS OF LIVING ORGANISMS. PLANTS AND ANIMALS

Biology is the science of living organisms, which include plants and animals, together with a number of simple forms of life which cannot be placed with certainty in either group. Living organisms of all kinds exhibit characteristics in which they contrast markedly with inanimate objects. They possess the power of growth, they reproduce their kind and they respond to various external influences in their environment.

The features of living organisms are due to the substance, *protoplasm*, which occurs in the form of microscopic units, or *cells*, of which an organism is built up, the larger forms of life consisting of millions of cells working harmoniously together.

Growth implies the capability of an organism to enlarge by the formation of new protoplasm, and this entails either the manufacture or the ingestion of food materials. Food materials are also consumed by the organism in order to provide the energy for its various activities, and during the consumption of food gaseous exchanges occur between the organism and the medium which surrounds it. The destruction of food within the organism to provide energy is called *respiration*, and, in the great majority of plants and animals, during this process oxygen is taken in and carbon dioxide is given out.

Reproduction means the formation of offspring essentially like the parent, and all organisms are capable of effecting this by some means. A typical plant, such as the broad bean plant, gives rise to seeds, which, on being sown, germinate and in due course produce plants like that which formed them. In animals, reproduction may be brought about, as in birds, by an egg which hatches under suitable conditions to form a new bird, or, as in the rabbit, by the birth of living young of the same essential form as the parent.

The response of living organisms to external factors is called *irritability*, as a result of which the organism may adjust itself to

changing conditions in its environment. The external factor is called a *stimulus* and, usually, the responses of animals to stimuli are more obvious than are those of plants. An animal, such as the frog, will react quickly to the stimulus of touch, and if the stimulus is of sufficient strength, the normal result is for the animal to change its position. Most plants do not respond obviously to the stimulus of touch, but do so to such stimuli as gravity, water and light. The well-known fact, that during the germination of seeds the shoot grows upwards to emerge from the soil, is an illustration of the response of that organ to gravity, and the details of the phenomenon will be considered in a later chapter.

Whilst plants and animals agree in possessing the fundamental features of living organisms they differ in several important characteristics which are set out below :

PLANTS

1. Are of indefinite growth, and grow at their extremities.
2. Only absorb fluids (both liquids and gases) and cannot ingest solid matter.
3. Possess organs which are green, owing to the presence of a pigment *chlorophyll*.
4. Because of the previous fact, plants can manufacture food from simple inorganic raw materials.
5. Are usually fixed in their environment.

ANIMALS

1. Grow to a mature size, mainly by equal growth all over the body.
2. Can take up solid food material, for which purpose they are provided with a mouth, or its equivalent.
3. Never possess chlorophyll.
4. Animals must be supplied with food material already elaborated.
5. Usually possess the power of locomotion.

The most important difference between plants and animals is the possession of chlorophyll by the former, as this enables plants to build up food from carbon dioxide and water, in the presence of light, a process described as *photosynthesis*. Animals cannot carry out photosynthesis, but must depend on food previously manufactured by green plants during that process. It is true, in fact, that, with the exception of a small group of microscopic organisms of the class known as Bacteria, all other forms of life are dependent directly or indirectly on the green plant. The nutrition of green plants is said to be *holophytic*, whilst that of animals is *holozoic*.

With regard to the differences between plants and animals enumerated above, it must be borne in mind that they apply only to

typical plants and animals, and exceptions to the general type occur in both groups.

A large group of plants, the Fungi (p. 144) consists of members which do not possess chlorophyll. Such forms cannot carry out photosynthesis, and therefore, like animals, depend on a supply of food previously elaborated by green plants.

The tapeworms and similar animals which live inside the bodies of other animals, possess no mouths, and take in fluids only, using the soluble food material from the digestive tract of the animal in which they occur.

Certain simple plants, such as *Chlamydomonas* (Fig. 61, A), which live in water, have the power of locomotion and swim about in response to various stimuli, whilst, on the other hand, some animals, including the corals and the sponges, have a fixed habit, being attached to the sea-bed.

Mention was made, earlier in the chapter, of organisms which cannot be classified as plants or animals. They are all microscopic and form a special group, the Protista. Some protists, allied to *Euglena* (p. 274), which is found in stagnant water, possess chlorophyll and are holophytic, but are also capable of ingesting solid food particles, and resemble animals in this respect.

As there is a vast assemblage of plants and animals in the world it is necessary to designate accurately each particular type or *species*. A species is an individual which exhibits certain characters peculiar to itself and which contrast with those of other species which may be closely related. A number of species which possess some common features may be grouped together to form a *genus*, and allied genera can be associated in *families*. For example, there are several species of mustard, which agree in possessing yellow flowers of characteristic structure (Fig. 1, B), but differ in the details of their fruits and other minute characters. The mustards are included in the genus *Brassica*, which also includes the cabbage and the turnip. Therefore, for accuracy it is essential that each species of *Brassica* should receive its own name. Although the use of common names is a popular practice in referring to plants and animals, it has little to commend it scientifically. It is often found that the common name assigned, for example, to a plant, is used elsewhere to describe a totally dissimilar species. The name 'sycamore' is used in Britain and the United States to indicate quite different plants, and, in biblical references, yet another plant is meant. Similarly the 'robin' of America is quite a distinct bird from our native species.

The scientific naming of plants and animals was standardised by the Swedish naturalist Linnæus (1707-78), who was the first to

attempt a classification of forms then known, into suitable groups for study. Linnæus assigned to each plant and animal two Latin or Latinised names, which were meant to indicate, to naturalists all over the world, the particular organism referred to, and since his time the practice has remained, and is invariably used in scientific literature. The white mustard is named *Brassica alba*, *Brassica* being its generic name, and *alba* its specific name. *Brassica*, however, designates a genus of plants, of which the members have common features, the individual species differing amongst themselves in smaller details. Each species of *Brassica* is distinguished from the others by the addition of a specific name, which must be used in conjunction with the generic name, because specific names may be common to very diverse genera. Thus, *Brassica nigra* is the black mustard, *Brassica arvensis*, the charlock, and *Populus nigra*, the black poplar, a common British tree.

In addition to the use of the **binomial system** of naming plants and animals, Linnæus made an attempt to create an orderly classification of these organisms. Up to his time there was little organised effort to classify accurately the known plants and animals, except in a very arbitrary manner. Linnæus arranged the species into genera, and the genera into larger groups which could accommodate new forms which might be discovered later.

The systematic classification of plants and animals is now an established fact, but at the present time more evidence of affinities is available than existed at the time of Linnæus. Whereas he used somewhat artificial characters (such as stamen number to delimit the plant groups), the modern classification attempts to arrange organisms into large groups, or **phyla**, which represent true 'blood' relationships. It is now generally accepted that all life arose from very simple ancestors, which in subsequent epochs, produced descendants of more complex form. This is the **theory of evolution**, which replaces the idea of **special creation**, which considers all existing plants and animals to have been created in their present form at the beginning of the world.

A **natural classification** embraces all the known forms of life, both existing and extinct, and the phyla and their subdivisions are arranged, as near as possible, to show an increasing complexity of structure, and to suggest the evolutionary advances made by each group.

An abridged classification of plants and animals is given on p. 391.

CHAPTER II

THE PLANT KINGDOM. THE WHITE MUSTARD PLANT. PLANT DURATION. HERBACEOUS AND WOODY PLANTS

The majority of common plants are members of the Angiospermæ, a group of highly organised plants possessing structures which enable them to live satisfactorily under the usual conditions found on land.

The White Mustard (*Brassica alba*, Fig. 1) may be taken as a typical example of the group as it displays all the usual features of such plants. It is a common herb of cultivation, being grown as fodder for farm animals, to provide the raw material for mustard and mustard oil, and for salads. It grows wild in several parts of Britain largely owing to the dispersal of seeds from cultivated plants which germinate readily under natural conditions.

The fully-grown plant consists of an axis, 18 inches to 3 feet in length, the lower part of which is embedded in the soil whilst the upper part is above ground and exposed to the atmosphere. That part in the soil is the **root system**, which, during its growth, is not exposed to light, and contrasts with the **shoot system**, above the soil, which receives light during the daytime.

The root system is concerned both with the anchorage of the plant and with the absorption of the dilute soil solution which provides the plant with water and various essential mineral elements. It consists of a main **tap root**, growing vertically downwards in the soil and bearing a number of branches or **lateral roots** which spread out into the surrounding soil. The lateral roots arise in a more or less regular manner, the youngest being nearest the apex of the tap root and the oldest uppermost, near to the soil level, a condition described as **acropetal succession**. This method of branching enables the root system to explore a new region of the soil as the elongation of the tap root continues at the tip.

The lateral roots may bear branches, or **rootlets**, which assist in providing satisfactory anchorage for the plant as the shoot system above ground continues its growth.

The younger parts of the tap root and its branches bear a cover-

THE WHITE MUSTARD PLANT

ing of *root-hairs*, concerned with the absorption of water and mineral salts from the soil particles with which they come into intimate contact.

The whole of the root system is characterised by the absence

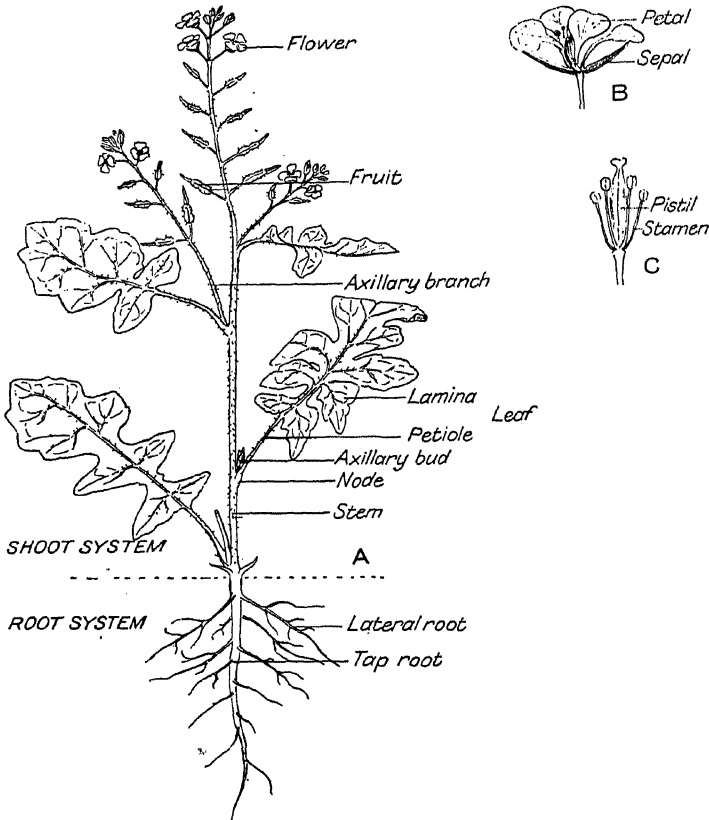


FIG. 1.—The White Mustard (*Brassica alba*).

A, entire plant $\times \frac{1}{8}$; B, flower $\times 1$; C, essential organs of flower $\times 2$; D, fruit $\times \frac{3}{8}$.

of chlorophyll, being of a white or brown colour. There is little difference in appearance between the main root and its branches, save that of size.

The shoot system consists of an erect main *stem* which is continuous with the tap root and bears a number of appendages, which, unlike the branches of the root system, are of several kinds.

At certain points of the stem green expanded *leaves* occur, the point of attachment of each being a *node*. The length of stem between two adjacent nodes is called an *internode*. Each leaf consists of a thin green expanded portion, the *lamina*, narrowing at its base to a thin stalk, or *petiole*, by means of which the leaf is attached to the stem. Owing to the presence of chlorophyll, the lamina is the chief food-manufacturing organ of the plant, carrying out photosynthesis during the daytime. The lamina is traversed by a series of *veins* concerned with the transport of watery solutions to the leaf and the removal of soluble food material manufactured there.

The arrangement of the veins is known as the *venation*. In the mustard, as the veins form a network, the venation is said to be *reticulate*, a feature of the group of plants known as Dicotyledons, and which contrasts with the usual *parallel* venation of Monocotyledon leaves such as those of the grasses. The shape of the lamina of the leaf may vary considerably amongst different species of plants (Fig. 2), but within narrow limits the general shape for any one species is constant. The lamina of the mustard leaf, although somewhat lobed, is in one piece, and is said to be *simple*, in contrast to leaves such as those of the rose, senna, and clover which are composed of a number of distinct leaflets and are said to be *compound*. The upper angle formed by the leaf with the stem is called the *axil* of the leaf, and in it occurs either an *axillary bud* or an axillary branch. The presence of this axillary structure is an important character of a leaf as it enables leaves of varying type to be identified as such.

A bud is a shoot system in an undeveloped condition, and consists of a compressed stem bearing a few rudimentary leaves. On the growth of the bud a lateral branch is formed, which, in all its essentials, is similar to the main shoot.

In the mature plant flowers will have been produced in groups or *inflorescences* at certain places on the shoot. A flower is a specialised shoot concerned with reproduction, as from it the reproductive bodies, or seeds, are formed.

It is usual to distinguish two classes of plant organs, viz. *vegetative organs*, consisting of roots, stems and leaves, concerned with nutrition, and *reproductive organs*, which are found in the flower.

The flowers of the mustard are small, and different stages in their development may be seen by an examination of the inflorescence. The flower-bud is enclosed by four yellow-green *sepals* which behave as protective scales until the flower expands, persisting afterwards around the lower parts of the four coloured

THE WHITE MUSTARD PLANT

petals (Fig. 1, B). The expanded petals are arranged in a cruciform manner, and each possesses an elongated claw held in position by the sepal. Within the petals are the reproductive parts of the flower (Fig. 1, c), consisting of six stalked bodies, the **stamens**, and a central elongated green **pistil**. The pistil encloses a number of minute **ovules** which may later develop into seeds.

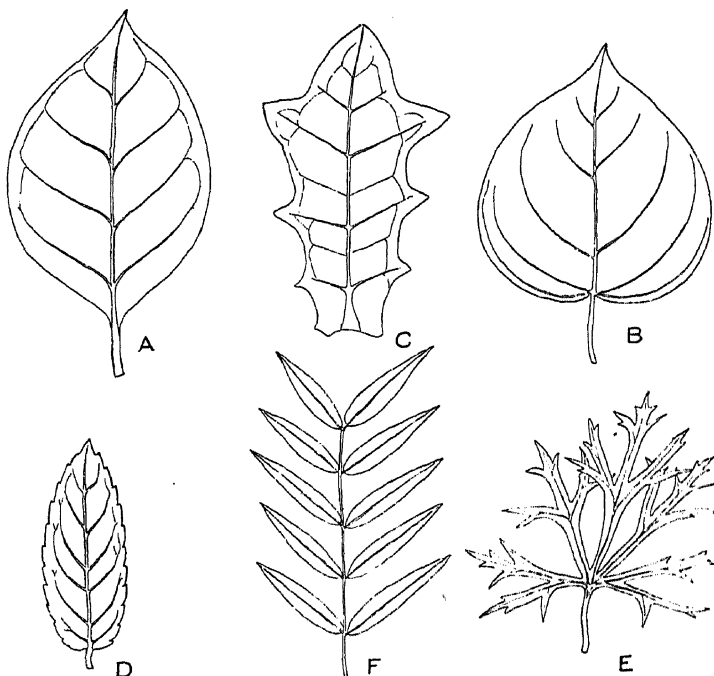


FIG. 2.—Leaf Shapes.

A, *Atropa Belladonna* (Deadly Nightshade); B, *Piper nigrum* (Black Pepper); C, *Hyoscyamus niger* (Henbane); D, *Mentha spicata* (Mint); E, *Aconitum napellus* (Monkshood); F, *Cassia acutifolia* (Senna) (all $\times \frac{1}{2}$).

If suitable specimens are examined it will be found that the pistil of the flower becomes the fruit, the other parts of the flower falling off shortly after the flower is fully expanded. The fruit (Fig. 1, D) is formed by a special part of the pistil, the **ovary**, the wall of which grows to form the **pericarp** or fruit-wall which accommodates the seeds. The mustard fruit takes the form of a slightly elongated beaked pod and is called a **siliqua**. On the ripening of the fruits, the mustard plant gradually dies, so that

after the dehiscence of the fruits to shed the seeds, they are the sole survivors of the plant which gave rise to them. Under suitable conditions the seeds germinate and in due course form a new generation.

Plant Duration. The life-cycle, or complete development of the mustard occupies one year, the seeds sown in spring developing into plants which die down completely in the following autumn when the seeds have been shed. Such a plant is called an *annual*, other examples of which include the garden pea and poppy.

Plant duration, however, can be more prolonged than that of the mustard and the life-cycle may extend over more than one season.

Plants like the onion, carrot, turnip and henbane require two seasons of growth in which to complete their life. During the first season they develop a vegetative system, in some part of which excess food is stored, after which the aerial part of the plant dies down at the approach of the unfavourable winter season. The plant does not die, but survives the winter as a dormant subterranean storage system. In the following spring the stored food is drawn on to produce a new aerial shoot system, which, during the summer, gives rise to flowers. On the production of fruits from these flowers at the end of the second season of growth, the parent plant is exhausted of its food material and dies down completely so that only the seeds survive the second winter. Such plants are called *biennials*, and they agree with annuals in that they produce but a single crop of seeds after which the parent plant succumbs.

A large number of plants have a period of growth extending over an indefinite number of years, during which time they produce numerous crops of seeds. Plants of this kind are called *perennials*, some of which live to a great age, as for example certain British oak trees which are several hundreds of years old, and the giant redwood trees of America, which may reach a thousand years or more.

There are two kinds of perennial, which differ in the behaviour of their aerial shoots.

Herbaceous perennials are those in which the shoot dies down to the ground level at the close of each growing season, to be replaced by an entirely new shoot in the next. These plants persist during the unfavourable season in the form of an underground storage organ in which food was stored during the previous season of growth to be used at the commencement of the next. Examples of perennial herbs include Solomon's seal (Fig. 11, A), iris (Fig. 11, B), deadly nightshade and daffodil.

Woody perennials contrast with the herbaceous type in that their aerial shoots do not die down, but persist above ground year after year, becoming more complicated each season, both by the addition of new branches and increased girth of their stems. The stems of all woody perennials are characterised by an external corky bark which prevents the loss of moisture from within and protects the shoot from the effects of low temperature. The buds of woody perennials differ from those of herbs as they are covered externally by corky bud-scales which protect the delicate young leaves within during the winter.

Woody perennials are either *deciduous* or *evergreen*. Deciduous trees and shrubs are those which shed their leaves at the approach of the unfavourable season and pass through this in a defoliated condition. The majority of British trees and shrubs such as the oak, horse chestnut, apple and hawthorn are of this type, but the deciduous habit occurs in certain tropical countries as well as in more temperate climates. In the monsoon forests of India a number of trees are deciduous, owing their habit to a regular alternation of dry and wet seasons. The leaves of deciduous trees are typically broad and thin and lose water readily to the dry atmosphere surrounding them. During the time that the root system is able to absorb a sufficiency of water to make up for that lost by the leaves, the plant is in no danger, but were the water supply to fail whilst the leaves continued to lose water the plant would die. The shedding of their leaves by deciduous plants is a means of conserving water within the plant during that period when absorption is difficult. It is clear that in the monsoon forest little water is available for the roots during the dry season, nor does it become so until the wet season commences. In Britain and other temperate countries, the deciduous habit is also due to a threatened water-shortage during the winter. In this case it is not a physical water-shortage which induces the plant to shed its leaves, but the fact that the low soil temperature during the winter restricts the absorption of water. Leaf-fall occurs before the actual onset of water-shortage. This means that although the deciduous habit enables some plants to exist under particular conditions, it was not necessarily developed by the plant in response to those conditions. In this country leaf-fall takes place in the early autumn, the preliminary stages having been going on for some time previously. Each leaf is severed from the stem by the development across the leaf-base of a tissue, the *absciss-layer*. When this plate of tissue dies the leaf may be readily detached with little force such as may be naturally provided by wind or rain. If leaf-fall were to consist only in the severance of the leaf, there

would be a considerable wound-surface formed over the large shoot system resulting in a large water-loss. In order to obviate this potential water-loss a layer of cork is formed beneath the absciss-layer, either along with its development or immediately after its completion, so that when the leaf is finally shed the wound is already sealed by a corky *leaf-scar* (Fig. 20, A) which is a prominent feature of the winter twig of deciduous trees.

Evergreen trees and shrubs do not shed the whole of their foliage at the end of the favourable season. The appearance in the winter of such plants as the pine, cypress, cherry laurel and holly differs little, if at all, from that in the summer, the leaves being retained throughout the year. Evergreen shoots usually possess leaves of a type that permits little water to be lost from them at any time, and this presumably means that the water required is less than that for deciduous trees of similar size, and the demand can be satisfied at all periods of the year. Evergreen leaves are often narrow and needle-like as in the pine (Fig. 78), or scale-like as in the cypress. They also have a skin or *epidermis* protected against water-loss by a thick layer of impervious *cuticle* (p. 49). Even when the leaves of evergreens are broad, as in the cherry laurel, and holly, owing to their cuticularised epidermis they lose less water than do deciduous leaves of equal area.

Evergreen plants do not retain their leaves indefinitely, but shed them in much the same way as deciduous trees after a period of from two to twenty years, according to the species.

From the point of view of seed-production, annual and biennial plants, producing but a single crop of seeds in their lifetime, are classed as *monocarpic*, in contrast to the perennial plants, which are *polycarpic*, as they bear many crops of seeds during their extended existence.

There are several plants, which although persisting vegetatively for a number of years, behave like annuals or biennials in that they die after giving rise to one crop of seeds. These plants are called *monocarpic perennials* and include the giant bamboo of India and the century plant (*Agave americana*) of Central America. The latter plant grows vegetatively for some years (often said to be one hundred, but usually considerably less) to form a large rosette of fleshy leaves. Ultimately it produces an elaborate inflorescence after which it dies completely.

CHAPTER III

THE STRUCTURE AND GERMINATION OF SEEDS

All members of the Spermatophyta, or Flowering-plants, are characterised by the production of seeds, which is the most common method by which they are disseminated, although many plants may supplement it by resorting to vegetative means of reproduction also. The seed is actually an undeveloped stage of the plant to which it gives rise, having been formed in a fruit which was derived from the pistil of a previous flower.

The nature and variation of the structure of the seed can best be studied by consideration of certain examples.

Broad Bean Seed (Fig. 3). This seed is produced in the characteristic fruit, known as a *pod* or *legume*, within which, attached to the inside wall by short fleshy stalks or *funicles*, are found several seeds. Each seed is a rounded discoid body, about one inch in diameter and varying in colour from greenish-white to brown. Externally, along one edge of the seed, is a dark scar, the *hilum*, which marks the former attachment of the seed to the funicle, and close to the hilum is a minute pore, the *micropyle*, which is readily found if a soaked seed is slightly squeezed. On removing the skin, or *testa*, from the seed the contained kernel is seen to be composed of two cream-coloured fleshy lobes, the *cotyledons*, held together by a slightly projecting peg-like body, the *radicle*, which is found to have been lying in a small pocket in the thick testa, with its apex near the micropyle. If the cotyledons are carefully separated, they are found to protect a small curved bud-like structure, the *plumule*, which is continuous with the radicle. The fleshy cotyledons can be shown to be rich in food material, for on placing a drop of iodine solution on them a blue-grey coloration denotes the presence of starch, and if tested with a drop of concentrated nitric acid followed by a drop of strong ammonium hydroxide, a deep yellow coloration indicates the presence of a nitrogenous material, protein, a characteristic food-reserve of seeds.

The radicle, plumule and cotyledons together comprise the *embryo* of the seed, cotyledons being modified leaves attached to the axis formed by the radicle and plumule.

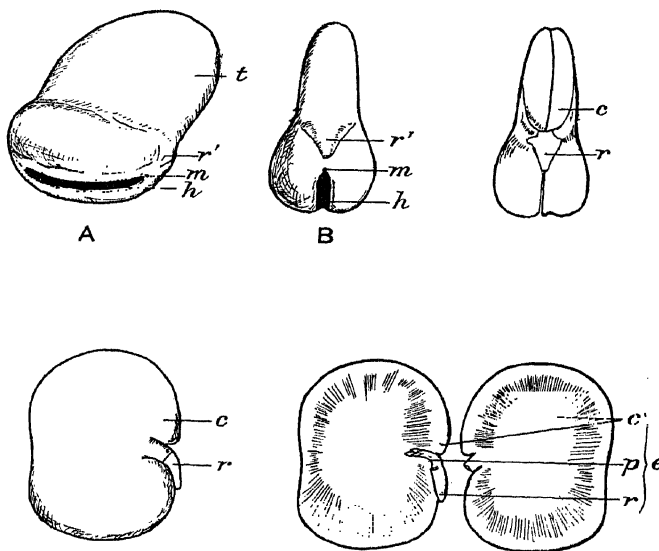


FIG. 3.—Broad Bean Seed.

A, B, external appearance; C, D, testa removed; E, cotyledons separated [all $\times 1$].

(c = cotyledon, e = embryo, h = hilum, m = micropyle, p = plumule, r = radicle, r' = radicle below testa, t = testa.)

Castor Oil Seed (Fig. 4). The fruit producing this seed is not so well known as the broad bean fruit (because the plant is not a native of Britain), but it is a spiny *capsule* with three compartments each of which contains one seed.

The seed is oval in shape, but varies in size from about half to three-quarters of an inch in length, and has a mottled brown testa. The micropyle is at the more pointed end, and is surrounded by a spongy outgrowth, the *caruncle*, which is shrunk in a dry seed, but swells up on soaking the seed in water. There is a minute scar on one of the flatter sides of the seed, close to the micropyle, and running from this, along the side of the testa, is a slight ridge, the *raphe*, which is a fusion of part of the funicle to the testa. The testa is hard and brittle, and on removing it a white entire kernel is found. Careful dissection of the kernel reveals an embryo, consisting of two thin veined cotyledons, closely pressed together, continuing towards the micropyle as a small radicle, and having between them a very minute plumule, the whole being embedded in a white tissue, the *endosperm*. The endosperm will be found

to contain protein, but no starch, on applying the above tests, but if the seed is rubbed on paper a greasy mark shows the presence

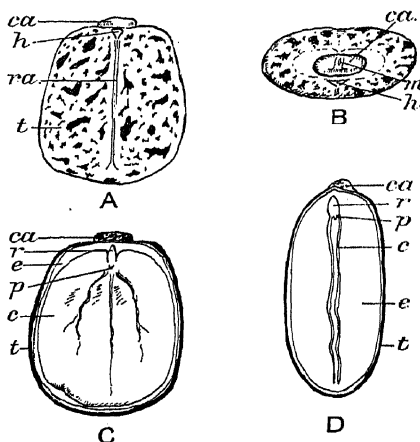


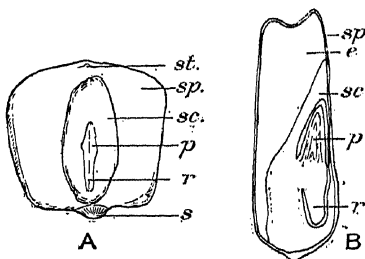
FIG. 4.—Castor Oil Seed.

A, external side view; B, external end view; C, longitudinal section of A, D, L.S. in plane and at right angles to cotyledons [all $\times 1$].

(*c* = cotyledon, *ca* = caruncle, *e* = endosperm, *h* = hilum, *m* = micropyle, *p* = plumule, *r* = radicle, *ra* = raphe, *t* = testa.)

of oil, which is an important food-reserve in this seed, and forms the familiar oil of commerce.

Maize Grain (Fig. 5). The maize grain is the fruit of the Indian



α. 5.—Maize Grain.

A, external view $\times 1$; B, longitudinal section $\times 1\frac{1}{2}$.

(*e* = endosperm, *p* = plumule enclosed in coleoptile, *r* = radicle enclosed in coleorhiza, *s* = scar of attachment to cob, *sc.* = scutellum, *sp.* = spermoderm, *st.* = stigma scar.)

corn, and is really a fruit containing a single seed. A large number of grains are attached to a pithy stem, forming a structure known as the **corn-cob**.

As the grain is a one-seeded fruit, the external features seen are not those of a seed, which occupies the entire cavity of the fruit so that the testa fuses with the fruit-wall forming a single skin, the *spermoderm*. The grain is a somewhat triangular flattened body, bearing a rough scar at the pointed end, where it was formerly attached to the cob, and a minute projection on the flat side near the broad end, the remains of the stigma. The spermoderm is transparent, and the seed inside is seen to have an oval area with a longitudinal ridge, on the side bearing the stigma-scar. This oval patch defines the limit of the embryo, the remainder of the kernel consisting of a white or yellow endosperm. By dissecting the grain, the embryo is found to consist of a fleshy oval part, in close contact with the endosperm, which is the *scutellum*, or main part of a single cotyledon, on the front of which lie the radicle and plumule protected by thin sheaths formed by the remainder of the cotyledon.

The food stored in the endosperm is starch and protein, a large part of the protein being confined to a layer immediately next to the spermoderm.

From the above description it will be noted that all the seeds examined possess an embryo, consisting of radicle, plumule and one or more cotyledons, and that the seed contains a reserve of food material, the whole being enclosed in a resistant skin, the testa. A seed is, therefore, an embryo plant, provided with food material to enable it to commence growth, and protected by a skin which enables it to remain living, though dormant, through such conditions as may be unfavourable to growth.

The variations in structure seen in the seeds illustrated, and which are the important variations for seeds in general, have to do with (i) the position of the stored food and (ii) the number of cotyledons possessed by the embryo.

The basis of **seed classification** is the position of stored food, two groups commonly being recognised, viz. *Endospermic Seeds*, such as the maize and castor oil, where the food is stored in a special tissue outside the embryo, and *Non-endospermic*, such as the broad bean, in which the cotyledons contain the food. The number of cotyledons is less important, but it is one character used in the classification of that group of flowering-plants, the Angiosperms, which are divided into *Dicotyledons*, the seeds of which usually possess two cotyledons, e.g. broad bean, castor oil, and *Monocotyledons*, in which the seed has one cotyledon, e.g. maize.

The more minute details of seeds may show more variation than has been here indicated, though the fundamental structure is the

same. The testa of the willow, poplar and willow herb is provided with fine silky hairs to assist in their dispersal by the wind : fleshy outgrowths, somewhat like the caruncle, may be developed, such as the bright red *arillus* of the yew, a development of the funicle, and the reticulate outgrowth of the micropyle which covers the nutmeg seed, forming the 'mace' of commerce ; the kernel may possess an infolded or *ruminated* endosperm, as in the nutmeg and the areca palm, whilst the number of cotyledons may be twelve or more in the pine and its relatives.

Factors influencing Seed Germination. The ultimate purpose of a seed is to produce a new plant, and sooner or later, given satisfactory conditions, it will proceed to do this. Usually, however, the seed remains dormant for some period before its development, but this period may show a considerable range, over which the seed can rest and still be capable of development.

Although much has been written about the longevity of seeds, it is now well established that some seeds, including willow and coltsfoot, remain viable for only a few days, whereas charlock and gorse seeds can lie dormant in the soil for forty years and still be capable of germination. Experiments on dry herbarium material have shown *Cassia bicapsularis* seeds to germinate after eighty-seven years and *Nelumbium* seeds after one hundred and fifty years. In most plants, however, the *viability* of the seed is not of long duration and the percentage of seeds germinating drops markedly after the first year.

Before a viable seed will germinate it must be provided with certain conditions, viz. a satisfactory amount of water, free oxygen and a suitable temperature. Seeds will remain in the dry state for an indefinite period, but on obtaining water they imbibe it, so causing the seed to swell. The main importance of water is that the protoplasm is enabled to enter an active state, and initiate the digestion of the food of the seed. Without a supply of free oxygen germination will not normally occur ; oxygen is required in the process of respiration during which food is broken down to supply energy for growth.

It should be noted that if soil water is so abundant as to fill up the pore spaces, so driving out the air, it is unlikely that seeds will germinate, and if a seed is planted too deeply in the soil, at such a level that oxygen-containing air does not diffuse, lack of germination may result. The temperature factor may vary according to the seed, but for any seed there is a minimum and maximum beyond which germination will not take place. Below the minimum a seed may remain dormant, though living, but beyond the maximum it is usual for the protoplasm of the seed to be killed.

For runner bean seeds the minimum temperature is about 9°C. , whereas rye will germinate at about 1°C. ; the maxima for these two seeds are about 46°C. and 36°C. respectively.

Light has recently been found to play some part in the germination of certain seeds, but at present the explanations are purely hypothetical.

Germination of Seeds. The stages passed through in the *germination* of a seed are the same for any particular species, though two general types of germination are met with.

If the broad bean seed is planted at a depth of 2 to 3 inches in the soil germination proceeds as soon as the requisite amount of water has been absorbed. The first organ to enlarge is the radicle, which elongates at the expense of food supplied from the cotyledons, and forcing its way through the testa, often in the vicinity of the micropyle, enters the soil. It will be found that no matter what may be the position of the seed, the radicle curves so that its tip is growing vertically downwards, a response to the stimulus of gravity, known as *geotropism* (Fig. 6, A). The radicle continues to elongate, giving rise to a main tap root which bears a covering of fine hairs a few millimetres from the tip. When the radicle is about 2 inches long the plumule has also commenced to elongate and it gradually emerges in a hooked form from between the cotyledons, being assisted by a slight elongation of the short cotyledon stalks (Fig. 6, B). On emergence the plumule curves so that its elongation proceeds upwards, also an instance of geotropism, though the plumule is *negatively geotropic* in contrast to the *positive geotropism* of the root. The plumule retains its hooked form in growing through the soil, as by this means the delicate tip is protected against mechanical injury as the young bud is drawn and not forced through the soil. The elongation of the root and plumule continues, the former producing lateral branches on its older parts, whilst the latter soon penetrates the soil surface, gradually erects its tip, and forms the shoot system (Fig. 6, C). On exposure to light the previously yellow shoot commences to form chlorophyll, and soon appears as a stem bearing leaves, those nearest the soil being modified as *prophylls* (Fig. 6, C) which are known to be true leaves because of their axillary buds.

As the seedling has been developing, the food has been withdrawn from the cotyledons, which on examination will be found to have a brown decayed appearance: at this stage, it is not unusual for the axils of the cotyledons to possess buds, which serves to emphasise that cotyledons are leaves modified for food storage.

The germination of the castor oil seed proceeds along slightly different lines. When the seed is planted, water taken up by the

18 STRUCTURE AND GERMINATION OF SEEDS

caruncle is passed through the micropyle to the kernel, and the embryo commences its growth, being provided with food from the endosperm. The radicle elongates and bursts the testa at the micropyle to emerge as the main root (Fig. 7, A). When the main

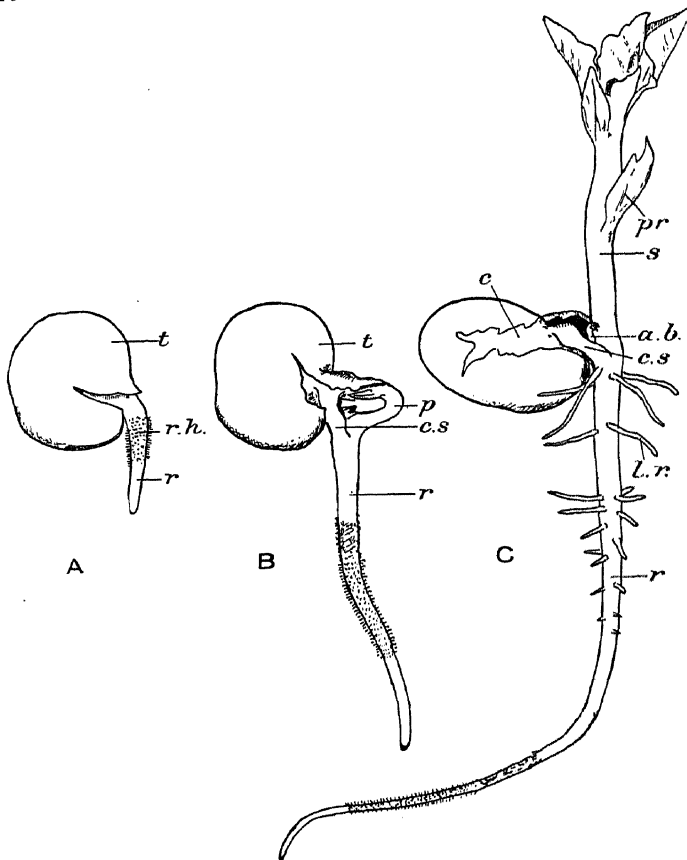
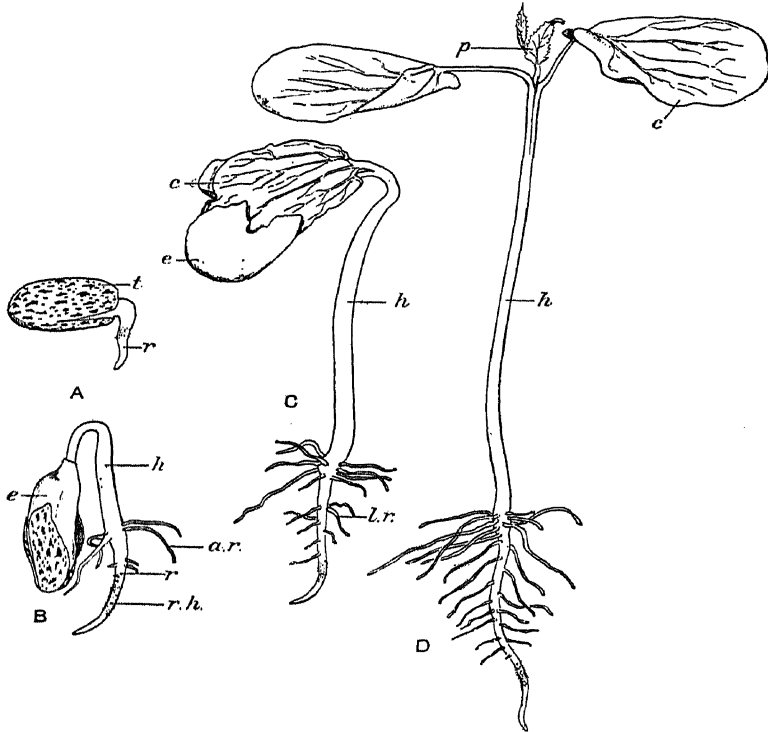


FIG. 6.—Stages in germination of Broad Bean Seed [$\times \frac{3}{4}$].

a.b. = bud in axil of cotyledon, *c* = cotyledon, *c.s.* = cotyledonary stalk, *l.r.* = lateral root, *p* = plumule, *p.r.* = prophyll, *r* = primary root, *r.h.* = root-hairs, *s* = stem, *t* = testa.)

root has become established a region at the top of the radicle, and immediately below the cotyledons, known as the **hypocotyl**, commences to elongate and produces a curved stem-like organ which is negatively geotropic (Fig. 7, B). The elongating hypocotyl withdraws the cotyledons and surrounding endosperm from the testa (or may carry up the whole seed), and carries them above

the soil (Fig. 7, c). The cotyledons, meanwhile, have been acting as digestive and suctorial organs, transferring the endosperm to the developing embryo. Above the soil the cotyledons continue to absorb the endosperm, but they also increase in area, so that they expand as the first leaves of the seedling, gradually developing chlorophyll as they receive light (Fig. 7, d). The plumule up to



3. 7.—Stages in germination of Castor Oil Seed.

A, B, $\times 1$; C, D, $\times \frac{1}{2}$.

(*a.r.* = adventitious root, *c* = cotyledon, *e* = endosperm, *h* = hypocotyl, *l.r.* = latera root, *p* = plumule forming shoot, *r* = primary root, *r.h.* = root-hairs, *t* = testa.)

this point has been protected in an undeveloped state between the cotyledons, but as the cotyledons separate the plumule begins its growth to produce the true stem bearing leaves, the later leaves differing in form from the elliptical cotyledons.

Amongst the Monocotyledons there is little variation in the method of germination and the development of the maize grain will suffice to illustrate the main features.

The grain, on planting, takes up water as in the other examples, and the embryo commences to produce the usual organs. The radicle elongates in its sheath, the *coleorhiza*, and on emergence through the spermoderm, breaks through the coleorhiza and forms the first root (Fig. 8, A). The emergence of the radicle is then followed by the production of one or two pairs of roots by the base of the plumule, such additional roots being said to be *adventitious* (Fig. 8, A). The plumule enclosed in its sheath, the *coleoptile*,

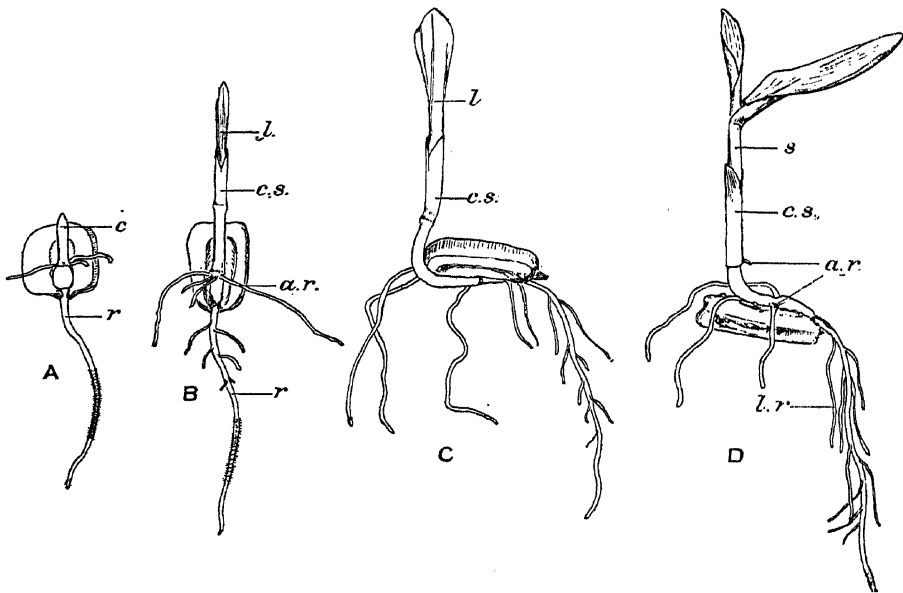


FIG. 8.—Stages in germination of Maize Grain [$\times 1$].

r. = adventitious root, *c* = coleoptile, enclosing plumule, *c.s.* = split coleoptile, *l* = first leaf, *l.r.* = lateral root, *r* = first root, *s* = shoot.)

elongates and grows upwards through the soil, the coleoptile forming a pointed structure which pierces the soil with ease and prevents injury to the delicate shoot within (Fig. 8, B). The food of the endosperm has been digested and absorbed by the scutellum which is closely applied to it. The root system is now found to consist of a tuft of roots, which includes that developed from the radicle together with the adventitious roots which have become equal to it (Fig. 8, C). The plumule emerges from the soil, and, having completed its protective function, the coleoptile stops elongating, so that the elongation of the shoot within ruptures it and the first

leaf emerges in a furred form (Fig. 8, c). In due course a stem bearing alternate leaves is produced, by which time the grain remaining in the soil has been depleted of its food.

The seedling types considered differ in one detail, viz. that in the case of the broad bean and the maize the cotyledons remain below the soil and never appear as leafy structures, whereas the cotyledons of the castor oil are carried above the soil and assume

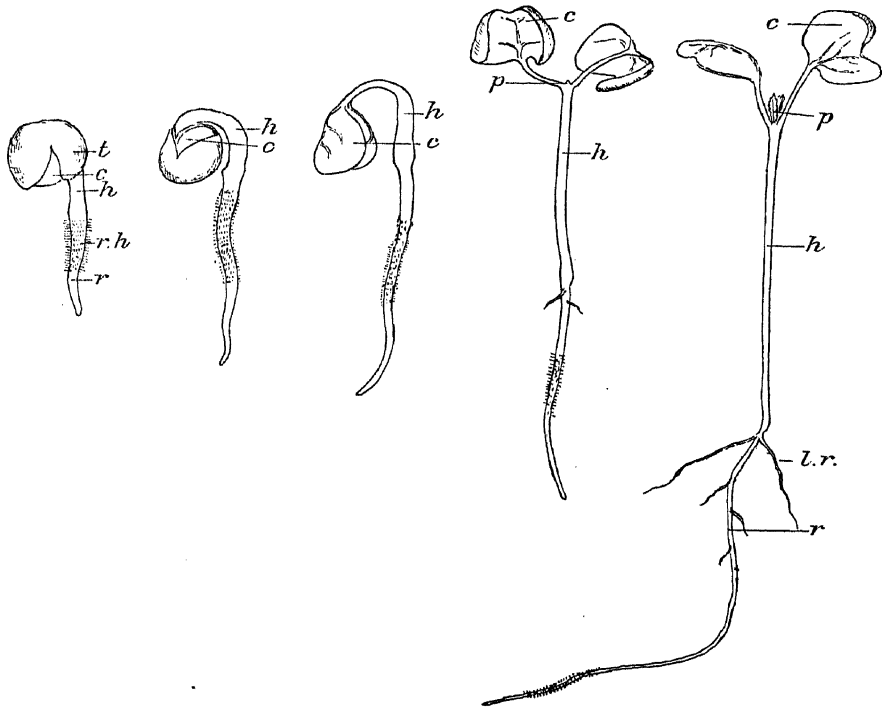


FIG. 9.—Stages in germination of Mustard Seed [$\times 3$].

(c = cotyledon, h = hypocotyl, l.r. = lateral root, p = plumule forming shoot, r = primary root, r.h. = root-hairs, t = testa.)

the form of foliage leaves. The former type, which is also exhibited by the oak, sycamore and date palm, is called *hypogeal*, whilst the latter, exhibited also by the mustard (Fig. 9), sunflower and vegetable marrow, is called *epigeal*. It should be remembered that in both types the first purpose of the cotyledons is concerned with food storage, the cotyledons being the actual organs of storage in non-endospermic seeds, whereas they are organs for the digestion and absorption of food in the endospermic seeds.

CHAPTER IV

MODIFICATIONS IN PLANT STRUCTURE CONNECTED WITH SPECIAL FUNCTIONS. PERENNATION. VEGETATIVE REPRODUCTION. CLIMBING SHOOTS. SPINY SHOOTS. BRANCHING OF THE SHOOT

In response to special needs, the vegetative organs of many plants may undergo modification in form.

Perennation

Perennation means the method by which a plant passes through a period unfavourable to growth, in such a manner as to be capable of development in the next favourable season.

Annual plants normally perennate by seeds only, but herbaceous perennials, and biennials at the end of their first season, perennate in a vegetative form. During the favourable season, which in Britain includes spring and summer, food is manufactured in excess of the immediate demands of the growing plant, the surplus food being stored in some organ which usually enlarges to accommodate it. The carrot stores food in a swollen tap root (Fig. 10, c) at the top of which is a compressed hypocotyl and stem. A bud of the stem produces the next season's shoot, drawing on the stored food to do so. The turnip and beet form structures similar to that of the carrot, but the swollen part of these plants is the hypocotyl, sometimes wrongly called the root. Adventitious roots become swollen for food storage in the lesser celandine (Fig. 16, B), monkshood and *Dahlia*. Such roots, or *root-tubers*, arise adventitiously in association with an axillary bud, either below ground or at ground-level, and, if they become detached from the parent plant, may form a means of vegetative reproduction.

In a large number of herbaceous perennials the stem and its branches form the organs of perennation, generally becoming swollen underground structures. The iris (Fig. 11, B) and Solomon's seal (Fig. 11, A) have fleshy underground stems, or *rhizomes*, which, in the growing season, send up aerial branches from their lateral buds. The iris rhizome is clothed with enveloping leaf-bases on its younger parts, whilst in the Solomon's seal the leaves are modified

to white scales or *cataphylls*, which are known to be leaves because of their axillary buds. Rhizomes are formed by ginger, male fern (Fig. 71, A) and *Podophyllum*.

In the crocus (Fig. 12) the main stem forms a tuberous underground body called a *corm*, by means of which the plant perennates. The dormant corm is clothed with brown scale-leaves with buds in their axils, the uppermost buds usually being larger than the others. When the corm commences growth in the late winter or

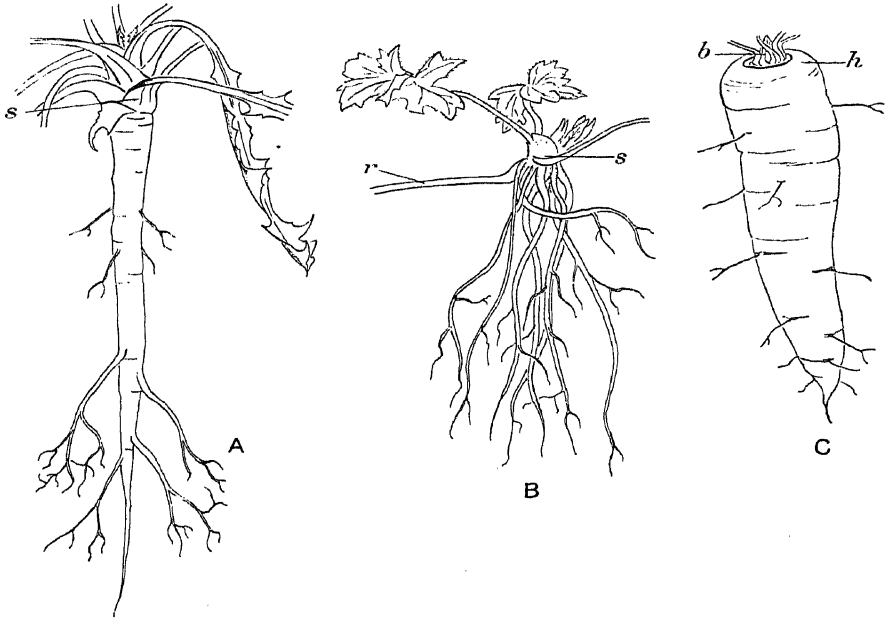


FIG. 10.—Root Systems.

A, tap root of Dandelion $\times \frac{1}{2}$; B, fibrous adventitious roots of runner of Creeping Buttercup $\times \frac{1}{2}$; C, storage tap root of Carrot $\times \frac{1}{2}$.

(b = bud, h = hypocotyl, r = runner, s = aerial shoot, with rosette habit.)

early spring, one or more of its buds elongates and produces a short stem bearing a tuft of narrow green leaves. After flowering, the leaves continue to manufacture food, and the surplus is stored in the stem of each aerial shoot, immediately above the parent-corm, which has been depleted of its food and presents a shrunk appearance (Fig. 12, E). In this way daughter-corms replace the parent each season, the bud-scales and the foliage leaf-bases remaining on the daughter-corm to form the brown scales mentioned at the beginning. Fibrous adventitious roots are formed at the base

of the parent-corm when it starts its growth. As the daughter-corms of the crocus are formed at a slightly higher level in the soil than the parent, after several seasons there would be the possibility of the new corms reaching the soil surface. This possibility is prevented by the development, at the base of the young corm forming

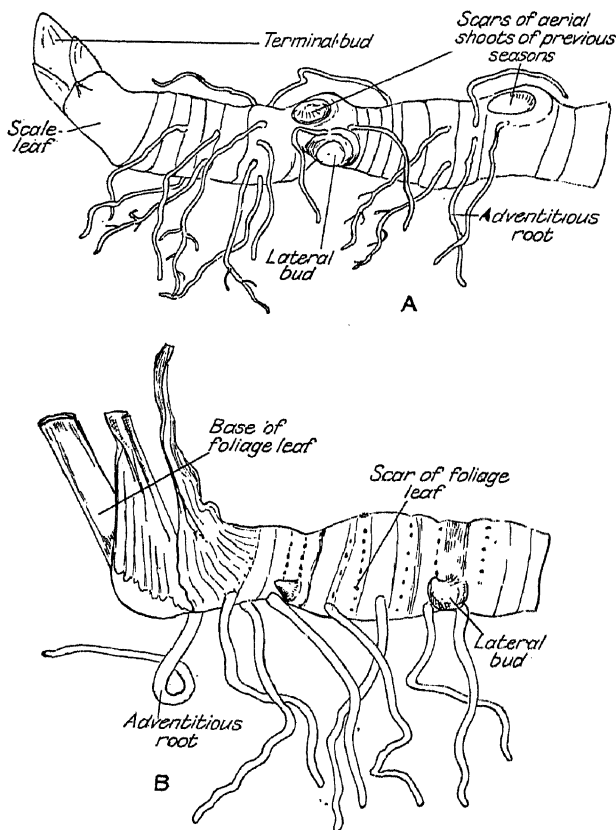


FIG. 11.—Rhizomes.
A, Solomon's Seal $\times 1$; B, Iris $\times \frac{1}{2}$.

on the parent, of one or more elongated fleshy roots, which, after becoming anchored at their tips, shrink longitudinally and pull the whole plant downwards. These *contractile roots* appear later as annulated structures (Fig. 12, E).

The autumn crocus (*Colchicum*, Fig. 113) forms a corm of slightly different origin from that of the crocus. Each corm bears a lateral

bud which in late summer develops a flower, only the perianth of which appears above ground, the ovary remaining below enclosed in the bud. After flowering, the corm remains dormant until the next spring, when the same bud that formed the flower sends up a leafy aerial shoot terminated by the fruit developed from the ovary of the flower of the previous season. During the growth in

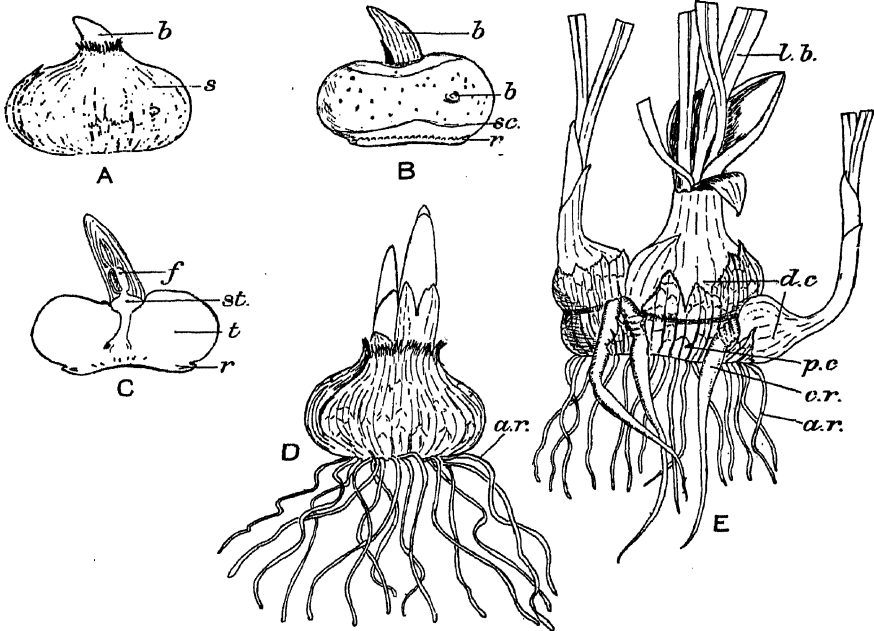


FIG. 12.—Corm of Crocus [all $\times \frac{2}{3}$].

A, external view; B, with scale-leaves removed; C, longitudinal section; D, early stage of growth; E, formation of daughter-corms.

(a.r. = fibrous adventitious root, b = bud, c.r. = contractile root, d.c. = daughter-corm, f = immature flower, l.b. = base of foliage leaf, p.c. = remains of parent-corm, r = rudimentary adventitious roots, s = protective scale-leaf, s.c. = scar of scale-leaf, st. = stem of bud, t = storage tissue.

the spring, the parent-corm loses its food reserves, and a daughter-corm arises laterally by the swelling of the basal part of the aerial stem, as in the crocus. Other plants which possess corms include *Gladiolus* and *Montbretia*, the parent-corm of the latter not being exhausted each season so that a chain of corms is formed over several seasons.

The potato plant survives the winter as a *stem-tuber* (Fig. 13, A), which is the swollen end of a thin underground stem, or *sucker*. The sucker arises in the axil of one of the lowest leaves of the aerial

shoot, or in the case of seedlings, from the axil of the cotyledon. The excess food formed during the summer by the green leaves is stored in the tips of the suckers which consequently swell. The resultant tuber is easily recognised as a modified stem for it bears

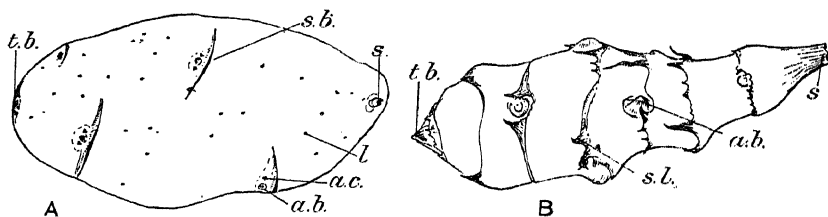


FIG. 13.—Stem-Tubers.

A, Potato $\times \frac{1}{2}$; B, Jerusalem Artichoke $\times \frac{1}{2}$.

(a.b. = bud in axil of scale leaf, a.c. = accessory bud, l = lenticel, s = scar of attachment to parent plant, s.l. = scale-leaf, t.b. = terminal bud.)

small scale-leaves with axillary buds, which constitute the so-called 'eyes.' Stem-tubers are also formed by the Jerusalem artichoke (Fig. 13, B), but in these the scale-leaves and buds are more obvious than those of the potato.

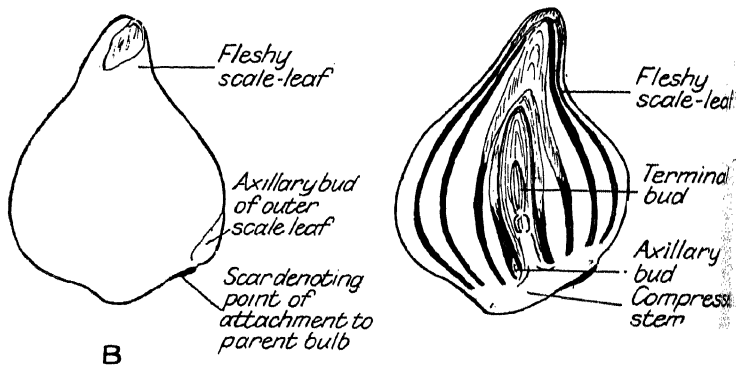


FIG. 14.—Tulip Bulb.

A, external appearance $\times 1$; B, with outer scale-leaf removed; C, L.S. of bulb.

Leaves are occasionally used as storage organs and form a swollen structure called a **bulb**. The bulb of the tulip (Fig. 14) is a swollen body enveloped by a brown scale-leaf. It consists of a compressed basal stem, the apex of which is occupied by a bud surrounded by a series of fleshy scales (Fig. 14, c). Each scale is a modified leaf for it has a bud in its axil. When the tulip bulb starts to develop

in early spring, adventitious roots arise from the base of the stem, and the central bud elongates, at the expense of the food in the scales, to form an aerial shoot. The aerial shoot consists of a long stem bearing several foliage leaves and terminates with a flower. The excess food manufactured by the foliage leaves is transferred to the scales of one or more of the axillary buds of the bulb, and these buds increase in size and become daughter-bulbs. By the end of the growing season, when the aerial shoot has died down, the original bulb is represented by several shrunken scales which enclose one or more daughter-bulbs of similar structure to the parent. As the bulb-scales are tubular and completely envelop those within, this type of bulb is said to be *tunicated*, in contrast to the *scaly* bulb of the lily in which the scales form an overlapping series.

The snowdrop is a bulbous plant, and although its bulb is tunicated, differs from the tulip in that the scales represent the fleshy bases of foliage leaves. Two green leaves are formed by the central bud of the snowdrop each season, and their bases swell to replace those of the previous season which formed the food-storing structures of the current season. Similar bulbs are found in daffodil, squill and onion, though the last is a biennial plant and forms a bulb only in its first season.

Mention must be made here of the perennation of woody perennials, which undergo little change in form throughout the year, persisting through the winter in a condition very similar to that of the active period. As mentioned in a previous chapter, evergreen plants retain their leaves in the winter, but deciduous plants lose their foliage. The persistent stems of both evergreen and woody trees are protected during the winter by a thick corky bark, and the buds are also protected by corky scales. The bud-scales of woody plants are either leaves or parts of leaves. In the ash, for example, the bud-scales are modified leaf-bases which can be ascertained on the opening of the buds in the spring when some bud-scales will be found to bear rudimentary laminæ at their apices. In the hazel and lime (*Tilia*), the majority of the bud-scales represent stipules, and will be found to occur in pairs at the bases of leaves when the bud expands.

Vegetative Reproduction

Reproduction is a characteristic of all plants. The Angiosperms normally produce offspring by means of seeds, but many supplement this by resorting to vegetative means, in which some vegetative part becomes detached to form a new plant.

Vegetative reproduction is more advantageous than reproduction

by seeds because the offspring are, as a rule, well established before separation from the parent. The method has, however, the disadvantage of limited dispersal, for whereas seeds are usually widely scattered, the daughter-plants formed by vegetative means are in close proximity to the parent with which they may compete.

In a number of herbaceous plants vegetative reproduction and perennation are effected by the same organ. Such structures as the stem-tuber, corm, root-tuber and bulb are often the commonest means of reproduction of those plants which possess them. The best-known example is the potato tuber, which, except in plant-breeding experiments, is the sole means of raising new crops. So usual is this that the small tubers planted each year are called 'seed-potatoes,' although they bear no relation to true seeds.

Rhizomes, too, may be a means of reproduction, even in the more fleshy types mentioned earlier in the chapter. Occasionally, the main rhizomes of the iris and Solomon's seal form lateral branches underground which may become detached later and establish new plants. In the couch grass and other grasses the rhizome is a thin elongated stem bearing whitish scale-leaves. This spreads rapidly and forms a ready means of reproduction.

Special organs formed naturally for purposes of vegetative reproduction include the *sucker*, the *runner* and the *bulbil*.

A sucker is a thin underground branch, arising either on a root or a stem, and growing to the surface gives rise to an aerial shoot. **Root-suckers** are formed by the plum, elm and rose, arising as adventitious buds on the roots. **Stem-suckers** arise either from the axils of scale-leaves on a rhizome, as in the mint (Fig. 15), or in a similar position on an older sucker as in the milfoil, a common weed of grassland.

The runner is a creeping aerial stem, which, arising as a slender axillary branch, runs along the surface of the soil, becomes anchored at its tip by adventitious roots, and forms a new plant by the growth of its apical bud. Plants with runners include the strawberry, which, in cultivation, is propagated only by this means, and the creeping buttercup (Fig. 10, B), a troublesome weed of cultivated land. In some plants, such as the common daisy, the runner is short and thick and is usually called an *offset*. Closely related to the runner is the *stolon*, which differs only in that it is not closely applied to the soil. The bramble forms long scrambling stolons, the tips of which ultimately take root at some distance from the parent.

Bulbils are generally modified axillary buds, although the term is applied to a variety of small tuberous structures concerned with reproduction. In the lesser celandine small whitish oval bulbils

arise in the axils of some leaves (Fig. 16, A). In the Welsh onion and some closely allied plants, the bulbils replace flowers of an inflorescence (Fig. 16, c). Some ferns, including *Asplenium bulbiferum* and *Tectaria cicutaria* produce bulbils adventitiously on their leaves, the bulbils generally falling off to continue their growth.

Although many plants in cultivation may propagate themselves vegetatively by natural methods, in addition artificial methods may be resorted to. A common horticultural practice is to raise such plants as the gooseberry, privet, *Pelargonium* and rose from **cuttings**. A cutting is a short branch of an aerial stem. Its cut

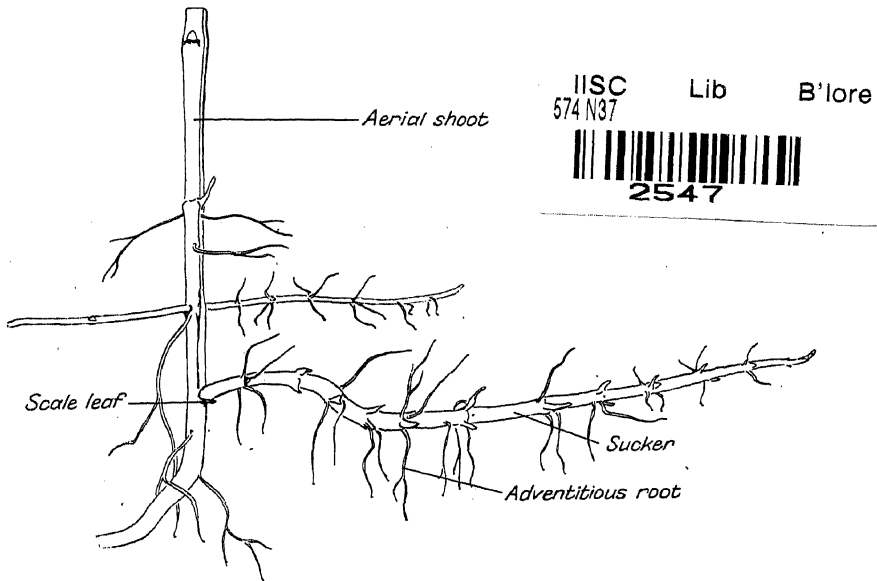


FIG. 15.—Sucker of Mint [$\times \frac{1}{2}$].

end is inserted in well-ventilated soil, so that in a short time, as the cut end heals, adventitious roots grow from the base of the stem and so establish a new plant. A variation of this method is to layer such plants as carnations and rhododendrons. Certain shoots are partly cut near a node and pegged to the soil. Adventitious roots form near the wound, and the rooted branch is then completely severed from the main plant. Sugar-cane plantations are commonly raised from cuttings; pieces of the stem are planted in furrows and covered with soil; they later sprout, and produce a yielding crop in about eight to ten months.

Artificial methods of vegetative reproduction may sometimes be

used because of the non-formation of seeds by the plant propagated or to bring to fruition a tree which is not in its full yielding condition. Seedless varieties of orange and other fruits are now of great commercial importance, but it is quite impossible to raise them from seed. In such plants, young plants of a seed-producing variety are grown from seeds and after a year or so buds of the seedless variety are grafted on to them. In due course these buds unite with the other plant, forming shoots, which will later give rise to seedless fruits. In the case of apples and pears, old trees of one variety can be used to bear another variety by grafting on

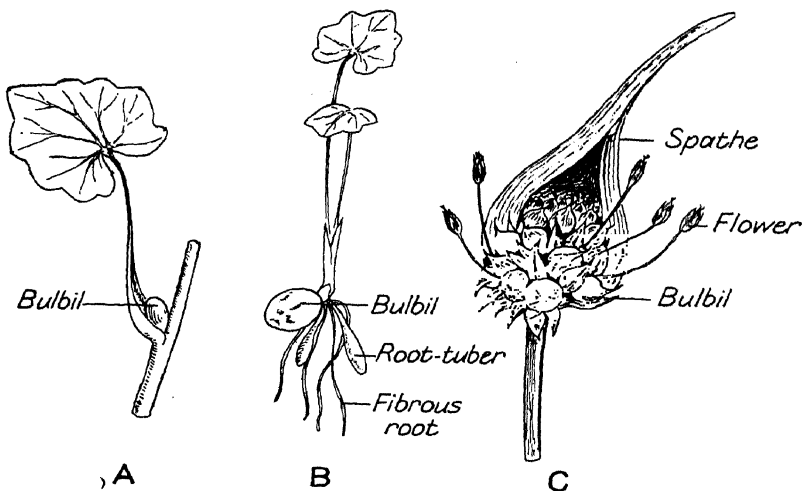


FIG. 16.—Bulbils.

A, Lesser Celandine; bulbil in axil of leaf $\times \frac{1}{2}$; B, bulbil of Lesser Celandine forming a new plant $\times 1$; C, bulbils replacing flowers in inflorescence of *Allium* $\times \frac{1}{2}$.

to the stem, or *stock*, of the old plant, young shoots, or *scions*, of the type required.

Grafting has wider applications than this, and may be the means by which a foreign tree can be encouraged to grow in a country which might otherwise be unsuitable. In many of the parks and botanical gardens of this country, oaks, cherries, and other species are grafted on to native stocks. Grafting may also be the means of overcoming a natural pest. The grape vine (*Vitis vinifera*) is liable to be attacked by a root louse (*Phylloxera*), but this may be overcome by grafting shoots of the vine on to stocks of another species (*Vitis Labrusca*), the roots of which are immune from the louse.

Climbing Shoots

Certain aerial stems have so little mechanical strength that they cannot remain upright without assistance. Weak stems must either remain prostrate or adopt a climbing habit.

The climbing habit is the better, for it enables the leaves to be satisfactorily exposed to the light, and the flowers to be suitably displayed. A prostrate stem is liable to be overgrown by erect plants in its vicinity which may result in its death.

By adopting a climbing habit, however, a plant loses some of its

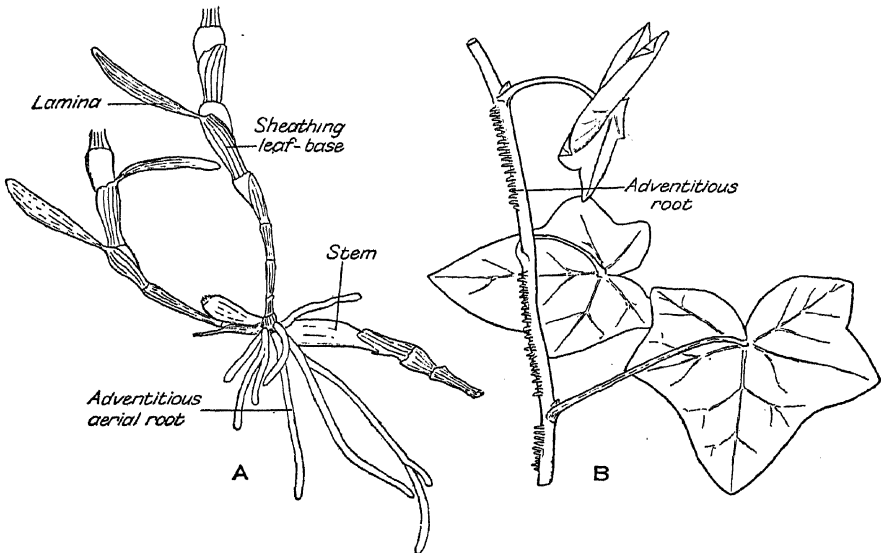


FIG. 17.—Aerial Root Systems.

A, absorbing roots of a tropical epiphytic Orchid $\times \frac{1}{3}$; B, climbing roots of Ivy $\times \frac{1}{2}$.

independence, for were its support to be broken down it would not regain the erect position unless another support were available.

A number of plants, including the hop, runner bean and bindweed, ascend more or less vertical supports by twining round them. The tips of the stems of these plants show a pronounced *circumnutation*, which means that they elongate in a spiral manner. When they come in contact with a solid support they remain closely applied to it in a series of coils, because the inner side of the stem against the support elongates less than the outside.

Twining plants have no particular modification of the shoot, as

is also the case in the ivy (Fig. 17, B) which climbs up walls and tree-trunks by forming short adventitious roots on its aerial stems close to the support. These *aerial roots* are only used for attachment, and if the stem is cut off from the normal root system in the soil it dies.

Climbing plants with little modification include *Tropæolum*, which climbs by means of sensitive twining petioles, and *Clematis* (Fig. 18, B) in which the petiole and the leaflet stalks are sensitive.

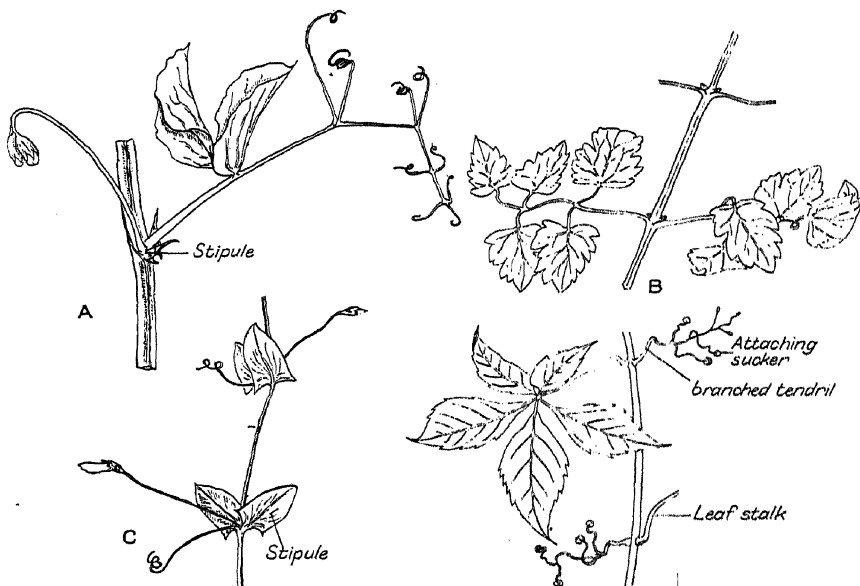


FIG. 18.—Climbing Shoot Systems.

A, leaflet-tendrils (Sweet Pea $\times \frac{1}{2}$); B, petiole-, and leaflet-stalk-tendrils (*Clematis* $\times \frac{1}{2}$); C, leaf-tendrils (Yellow Vetchling $\times \frac{1}{2}$); D, stem-tendrils (Virginian Creeper $\times \frac{1}{2}$).

The majority of climbing plants develop special organs, or *tendrils*, by which they attach themselves to supports. Tendrils are sensitive organs which behave characteristically on coming in contact with a solid support. They are modified parts of the shoot system and are generally elongated filamentous structures.

In the garden pea, sweet pea (Fig. 18, A) and vetch, which all possess compound leaves, the terminal leaflet and the uppermost lateral leaflets form green unbranched tendrils the tips of which coil round thin supports. The entire lamina of the leaf of the yellow vetchling (*Lathyrus aphaca*, Fig. 18, c) forms an unbranched

tendrils, but as this deprives the plant of much of its photosynthetic surface, the stipules become expanded and green and carry out the usual work of the lamina.

Stipular tendrils are not common, but are possessed by a tropical woody climber, *Bauhinia*, a member of the family Leguminosæ. Another tropical climber, *Gloriosa superba*, climbs by means of a much elongated leaf-tip which acts as a tendril.

Axillary branches may be modified as tendrils, and their true nature is ascertained by their position relative to the leaf. In the vegetable marrow, bryony (*Bryonia*) and the passion-flower, long unbranched stem-tendrils are formed. Before meeting a support these tendrils are uncoiled but on reaching the support, the tips encircle it, and the stimulus of contact results in their coiling from both ends to form a spring-like attachment. It may be that this coiled tendril permits the plant to be pulled away from its support without damage to the tendril.

The Virginian creeper (Fig. 18, D) climbs by means of branched tendrils which become attached by sucker-like tips to such supports as walls, fences and other vertical surfaces. The tendril represents the apex of a stem of limited growth, the vegetative shoot being continued by the elongation of the uppermost axillary branch.

Tendrils of similar origin are found in the vine, but in this example the tendrils are attached by coiling.

Another type of climber is the plant with a scrambling habit. Scrambling plants with weak stems produce superficial outgrowths which act like hooks and enable the stem to grapple with other plants. The bramble and dog-rose form hard prickles on their stems, leaf-stalks, and, frequently, veins. Each prickle has a hooked form, the point being directed towards the point of origin of the branch on which it occurs, and it enables the stem to be loosely attached to plants and other structures over which it scrambles. In the goosegrass, the stems and leaf-stalks bear small hooked hairs which serve the same purpose as prickles.

Spiny Shoots

The aerial shoots of a number of plants bear pointed outgrowths, or *spines*, which might be thought to be a defence against grazing animals. Although the spiny habit does tend to protect the plant from the attacks of animals, it is probable that it is more concerned with the prevention of water-loss from the shoot. The best examples of spiny shoots are found in plants inhabiting dry regions, such as deserts, and sandy soils which retain little water. In such plants the spininess is produced by a reduction of the leaf-surface, broad leaves being absent.

Reduction of leaf-surface must result in some reduction of water-loss, and therefore may enable a plant to tolerate drier conditions than could plants with broader leaves.

It is true, however, that spines are found on plants with broad leaves and which do not suffer a lack of water, so that it is difficult to explain the habit in all plants.

Spines are always modifications either of leaves or stems, and

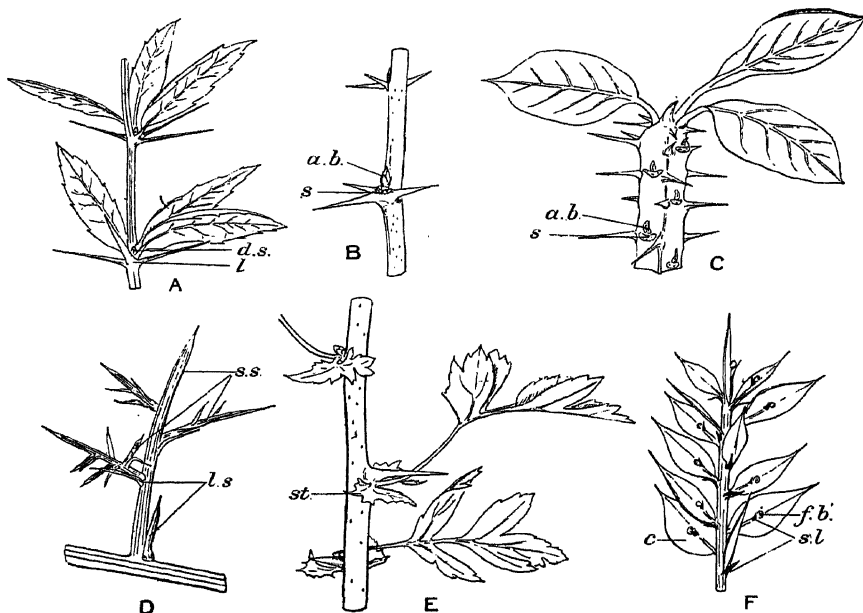


FIG. 19.—Spiny Shoot System [all $\times \frac{1}{2}$].

A, leaf-spines (Barberry); B, leaf-base spines (Gooseberry); C, stipular spines (*Euphorbia splendens*); D, leaf- and stem-spines (Gorse); E, stem-spines (Hawthorn); F, spiny cladodes (Butcher's Broom).

(a.b. = axillary bud, c = cladode, d.s. = axillary dwarf-shoot, f.b. = flower bud, l = 3-forked leaf-spine, l.s. = leaf-spine, s = leaf-scar, s.l. = scale-leaf, s.s. = stem-spine, st. = stipule.)

are arranged in a definite order on the shoot. They are not to be confused with prickles which are arranged haphazardly and are always superficial, whereas the tissue of a spine is continuous with the inner tissue of the shoot which bears it.

Leaf-spines are distinguished by the presence of axillary buds or shoots. In the barberry (Fig. 19, A), the leaves of the main stems each form a group of spines bearing a dwarf-shoot with foliage leaves in the axil. The leaves of many Cacti are reduced to spiny groups, broad leaves being completely suppressed.

The spines of the gooseberry (Fig. 19, B) are outgrowths of the leaf-bases, and persist fused to the stem when the rest of the leaf is shed in the autumn. Stipular spines are found in several species of *Euphorbia* (Fig. 19, c) and in the false acacia (*Robinia*).

Stem-spines, which are of axillary origin, are found in the gorse, which also possesses leaf-spines (Fig. 19, D). The hawthorn (Fig. 19, E) and sloe bear sharp woody stem-spines which may bear foliage leaves and buds.

In those plants with extreme reduction of leaf-surface, such as the gorse, in Britain, and the cacti and species of *Euphorbia* of warmer regions, the lack of green tissue is made up, in some measure, by the pronounced development of chlorophyll by the stems.

Another interesting British plant showing such green stems is the butcher's broom (*Ruscus*, Fig. 19, F) the leaves of which have become small black scales, in the axils of which flattened leaf-like stems are formed. These leaf-like branches are called **cladodes**. They are known to be stems, not only because of their axillary position, but because they bear minute scale-leaves in the axils of which flower-buds are found.

Cladodes should not be confused with **phyllodes** which are expanded petioles found in certain species of *Acacia* and *Oxalis*, and carry out the work of the lamina which is either much reduced, or completely absent.

Branching of the Shoot

The typical Angiosperm stem is characterised by branches, except in rare cases such as some Monocotyledons, exemplified by the palms. Owing to the fact that lateral branches are formed from axillary buds, their arrangement bears some relation to that of the leaves, known as **phyllotaxis**, which is typical for any particular plant.

The general appearance of the shoot is largely decided by the behaviour of its apex which usually takes the form of a terminal bud. For example, in the pine and the ash, the terminal bud elongates each season to add a new length of shoot to that already existing, whilst the lateral buds produce branches which remain subsidiary to the main stem. Such a system of branching is called a **monopodium**, which is not only found in the examples cited, but also in the erect shoots of many annual herbs, and in rhizomes such as that of the wood sorrel.

In many trees, including the willow (Fig. 20, B) and the elm, the terminal bud does not continue the main axis each year owing to its death in the late summer. The elongation of the stem, in

this case, is continued by a lateral bud, and the lateral branches produced in successive seasons form a shoot called a *sympodium*.

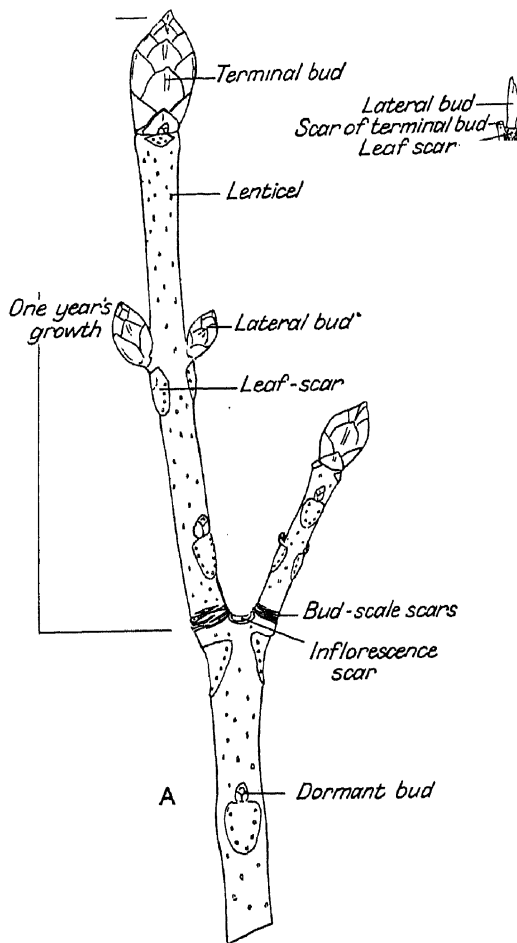


FIG. 20.—Winter Twigs.

A, Horse-chestnut; B, Willow
[$\times \frac{1}{2}$].

The sympodium may appear to be a continuous axis although it is actually a series of lateral branches. This is seen in the rhizome of the Solomon's seal (Fig. 11, A), in which the terminal bud of the current season forms an aerial shoot, the elongation of the rhizome underground being continued by a lateral bud of the aerial stem which dies at the end of the season.

In some trees both monopodial and sympodial branching may occur. This is the case in the horse-chestnut (Fig. 20, A) when, if the terminal bud is vegetative, monopodial branching results, but when the terminal bud contains an apical inflorescence this ends the elongation of that particular branch, and growth in the next

season is continued by the uppermost lateral buds which give rise to a forked shoot.

CHAPTER V

THE PLANT CELL. CELL-DIVISION. DIFFERENTIATION OF PLANT CELLS. SIMPLE TISSUES

The Plant Cell

The plant has been considered, so far, as an organism of characteristic form, consisting of a number of organs concerned with important nutritional and reproductive functions. The features of any living organism are due to its intimate structure, which has already been said to be composed of microscopic cells.

One of the earliest scientists to describe the minute structure of plants was Robert Hooke, who, in 1665, using a microscope of his own design, examined various substances, including thin slices of bottle cork, obtained from a certain oak tree. Hooke was impressed with the similarity in appearance between cork and a honeycomb, and consequently applied the term 'cell' to the component units of cork. The term 'cell' has been used since then to describe the unit of plant and animal structure, but whereas, in cork, Hooke was seeing but the dead skeleton, the modern idea of the cell emphasises the living substance, protoplasm, discovered by von Mohl in 1846.

The mature plant cell presents certain features which can be seen on the microscopic examination of the inner skin of the fleshy scale of an onion bulb. The skin is seen to consist of a number of tabular cells fitting compactly together (Fig. 21, A) to form a *tissue*, the components being separated by thin membranes. If the tissue is examined more closely (Fig. 21, B), each cell is found to be bounded by a *cell-wall*, lined with a thin layer of greyish granular *cytoplasm*, situated in which is a round or oval *nucleus*. The cytoplasm and nucleus, together constitute the *protoplast*, which takes the form, in this cell, of a thin envelope surrounding a central space, the *vacuole*, occupied by a watery *cell-sap*.

The cell-wall is composed of a carbohydrate substance *cellulose* (Chap. IX) which is characteristic of plants. Cellulose is distinguished by its solubility in cuprammonia (ammoniacal solution of copper oxide), and its blue coloration after treatment with strong sulphuric acid and iodine solution. The cell-wall is a secondary

structure formed by the living protoplast, which generally adds new substance to the wall during the life of the cell.

Protoplasm is not a simple substance but a complex mixture of substances which form what is called a *colloidal system*. Colloidal substances include gelatine and starch, and contrast with *crystalloids* such as sugar, sodium chloride and other mineral salts, in a number of ways. Whilst crystalloids can form true solutions in which the solute particles are of molecular or ionic size, colloids cannot form true solutions. If, for example, gelatine is placed in warm water it dissolves and forms a solution called a *sol*. A colloidal sol differs from a crystalloid solution in that its dissolved particles, consisting of aggregates of molecules, are of larger size. The solute particles of a true solution can readily

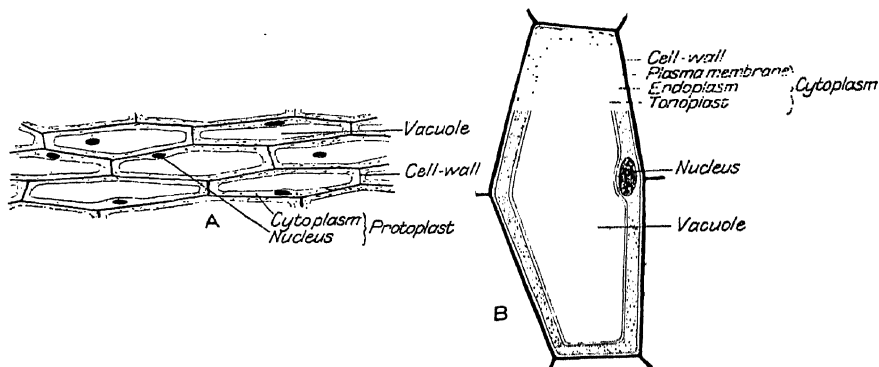


FIG. 21.

A, surface view of part of epidermis of fleshy scale of onion bulb ; B, single cell, more highly magnified.

pass through such membranes as parchment and animal bladder, but colloidal particles are unable to do so. If a gelatine sol is allowed to cool it sets as a relatively firm jelly, or *gel*, which consists of a matrix of gelatine enclosing droplets of water. All colloidal systems are composed of two *phases*, viz. a *continuous* phase, through which are dispersed particles or droplets of a *dispersed* phase. In a gelatine sol, the continuous phase is water and the dispersed phase, particles of gelatine, but in the gel state, the dispersed phase consists of water enclosed in the continuous phase of gelatine. This reversal of phases is of common occurrence amongst those colloidal systems known as *emulsoids*, in which both phases are fluid, and which differ from *suspensoids* (e.g. colloidal gold, silver and iron) in which the dispersed particles are solid.

In the active cells of normal vegetative organs, the protoplast is mainly in the form of an emulsoid sol, consisting of a watery solution of sugars, salts and organic acids, dispersed in which are protein (Chap. IX) particles. The amount of water in active protoplasm is about 80 per cent. In dormant cells, such as those of seeds and spores, the protoplasm usually contains less water and forms a gel.

The cytoplasm of a vacuolated cell, like that of the onion scale, is not homogeneous, but appears to be bounded by two very thin membranes within which is a wider granular zone. The clear membrane next to the cell-wall is the *plasma membrane*, that next the vacuole is the *tonoplast*, and between the two is the *endoplasm* (Fig. 21, B). The plasma membrane and tonoplast are believed to differ in composition from the rest of the cytoplasm, and probably consist of protein together with certain fatty substances called lipoids.

In some active cells the cytoplasm exhibits the phenomenon of 'streaming,' which is a flowing of the endoplasm in a characteristic manner through the cell. This may be observed in the cells of the leaves of the Canadian pondweed (*Elodea*) in which the cytoplasm follows a path within the cell-wall, and is said to 'rotate,' and in the staminal hairs of the spiderwort (*Tradescantia*) in which the cytoplasm 'circulates' or streams along certain strands to arrive back at the point from which it started. The streaming of protoplasm probably plays a part in nutrition for it is usually most active at temperatures which are best for the other activities of the cell.

The nucleus (Fig. 24, A) is a specialised part of the protoplast which plays an important part in the formation of new cells, and appears to control the general activities of the cell. It is delimited from the rest of the protoplast by a delicate *nuclear-membrane*, enclosing the other characteristic structures. The details of the nucleus have been largely studied in cells which have been killed and stained to emphasise their structure. It should be remembered, that, although such cells manifest features which, in all probability, represent structures in the living nucleus, some of these features may not be present in living cells, but have arisen during the treatment.

Within the membrane of such a stained nucleus is the *nucleoplasm*, appearing as a network of fine fibres, parts of which stain readily with dyes like safranin, and are known as *chromatin*, the rest of the network being the *linin*. In the nucleoplasm are one or more small round bodies, the *nucleoli*, the importance of which has not, so far, been decided.

The cell-sap is a watery solution of sugars, mineral salts, organic acids and their salts, some of which exist in true solution and others in colloidal solution. It is commonly colourless, but in some tissues, such as those of the beetroot, and petals of red and blue colour, the sap is coloured owing to the presence of substances called *anthocyanins*. The cell-sap is of considerable importance, for not only is it a reservoir of food and raw materials, but it plays a great part in the absorption, by the cell, of water and nutrient materials.

Plant cells, in general, present the features so far described, but other structures may also be present. Frequently the cytoplasm is characterised by small bodies, the *plastids*, which are concerned with the nutrition of the cell. Plastids are parts of the living protoplast, and are conveniently classed on their coloration, which corresponds with their functions in the cell.

The green colour of some plant organs is due to the presence of *chloroplasts*. Chloroplasts owe their green colour to two pigments, chlorophyll *a* and chlorophyll *b*, which are formed only in daylight, and when the plant is supplied with iron, magnesium and some other elements. The chlorophylls are accompanied by two yellow pigments, carotin and xanthophyll, but these are not dependent on light for their formation. Chloroplasts are of great importance as they are concerned with the absorption of light energy in the process of photosynthesis. They vary considerably in size, shape, and number per cell in various plants. In many leaves (Fig. 43, B) they occur as numerous small discoid plastids in each cell, but in the Green Algæ (Chap. XII) they are fewer, and so specialised as to form an aid in identification. For example, the alga *Chlamydomonas* (Fig. 61, A) a unicellular plant, has one basin-shaped chloroplast in each cell, and *Spirogyra* (Fig. 63, A) a filamentous alga, has one or more spirally-wound, ribbon-like chloroplasts in each cell.

Chromoplasts are yellow or red plastids occurring in a variety of organs, such as the ripe tomato fruit, the root of the carrot, and the petals of the buttercup flower. They contain either carotin or xanthophyll or both. The part played by chromoplasts is obscure, for though their presence in petals and succulent fruits may be of attractive use, their presence in underground organs is not easily explained. In some organs, chromoplasts have developed from previous chloroplasts, as may be realised by studying the ripening of the green fruit of the tomato or the rose.

Leucoplasts are colourless plastids which occur in young cells and in storage organs. It is usual to refer to all colourless plastids as leucoplasts, no matter what their possible function may be.

One of the best known is the *amyloplast*, present in starch-storing organs like the potato tuber, and concerned in the transformation of sugar to starch. Occasionally leucoplasts may become chloroplasts on exposure to light. This is found in the potato tuber, which, if exposed to light for several weeks, becomes green because the leucoplasts of its outer cells form chlorophyll.

The origin of plastids in the cell is not fully understood, for, whilst the chloroplasts of some moss leaves multiply by division, there is evidence that plastids arise during the maturation of cells from minute proplastids present in the young cell.

Many plant cells contain non-living *inclusions*, which may be *food-bodies* or *by-products*. Food-bodies, which include granules of starch and protein and droplets of oil, are of further use in the nutrition of the plant, but by-products are not, and include calcium oxalate and carbonate.

Starch grains are of wide occurrence in plants, being present in the cytoplasm of diverse organs and tissues. They consist of colourless insoluble granules of varying size and shape, and reach their maximum development in storage organs such as tubers and corms, and in seeds such as the maize and wheat. In many cases the grain has a central spot, the *hilum*, around which the grain was built up in a series of layers, or *striations*. Generally speaking, the features of the starch grains of a particular plant species are so distinctive that they may be used in the identification of drugs and cereals in powder form (Fig. 22).

Protein occurs in storage organs, particularly seeds, in the form of *aleurone grains*. Aleurone grains are often of small size and present no special features as in the cotyledons of the pea and bean, but in oily seeds they are larger and more elaborate. The aleurone grains of the endosperm of the castor oil seed (Fig. 22, r) are oval, and consist of amorphous protein in which are embedded a large angular *crystalloid*, and one or more smaller *globoids*. The matrix and the crystalloid consist entirely of protein, but the globoid contains, in addition to protein, a double phosphate of calcium and magnesium. Somewhat similar aleurone grains are found in the cotyledons of the almond seed and in the endosperm of the Brazil nut. The seeds of some members of the family Umbelliferae possess small aleurone grains containing a small crystal of calcium oxalate.

Calcium oxalate is a very common by-product in plant cells, occurring in various crystalline forms. It is probably formed by the neutralisation of oxalic acid, a common product in plant metabolism, with calcium salts, and its insoluble nature renders it innocuous which would not be the case if the acid were to accumu-

late. The variety of form and the persistent nature of calcium oxalate make it a useful aid in the identification of powdered drugs. In senna leaflet, and *Quillaria* bark, its crystals are large simple **prisms** (Fig. 23, A); in squill bulb certain cells contain bundles

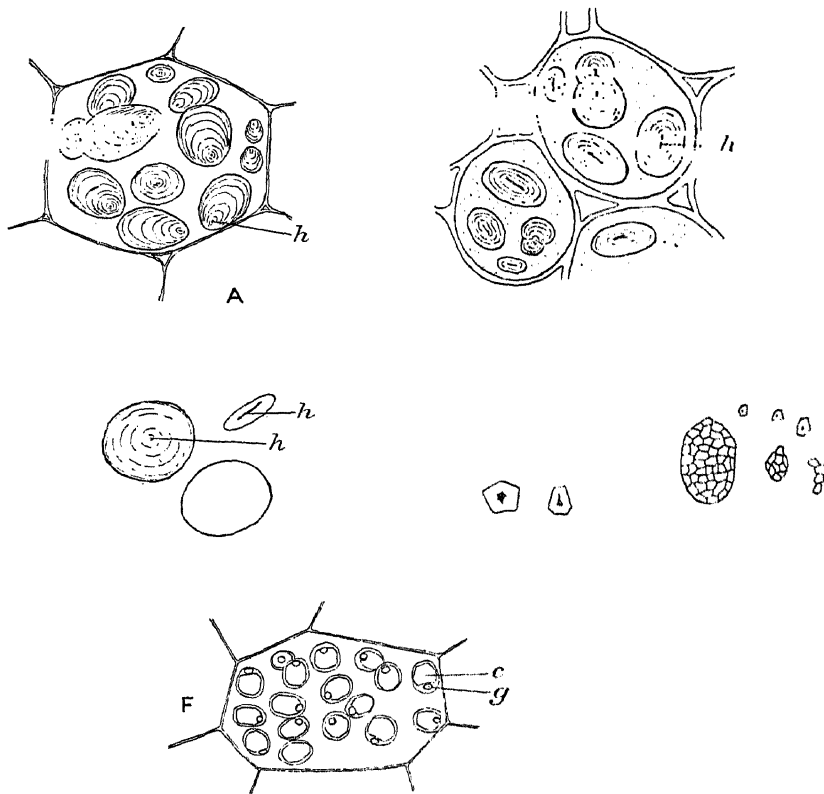


FIG. 22.—Food Reserves.

Starch: A, in cell of Potato tuber; B, in cells of cotyledon of Pea; C, starch grains of Wheat; D, of Maize; E, of Rice.

(h = hilum.)

Protein: F, aleurone grains in cell of endosperm of Castor Oil seed.

(c = crystalloid, g = globoid.)

of needle-like crystals, or **raphides** (Fig. 23, D); in henbane leaf, senna leaflet and the various organs of the rhubarb plant, the crystals form aggregates or **rosettes** (Fig. 23, B, C), whilst in the root and leaf of *Atropa Belladonna*, certain cells are filled with minute crystals, or **crystal sand** (Fig. 23, E).

Calcium oxalate is identified by its insolubility in acetic acid, and solubility in hydrochloric acid, without effervescence. These reactions serve to distinguish it from another mineral by-product,

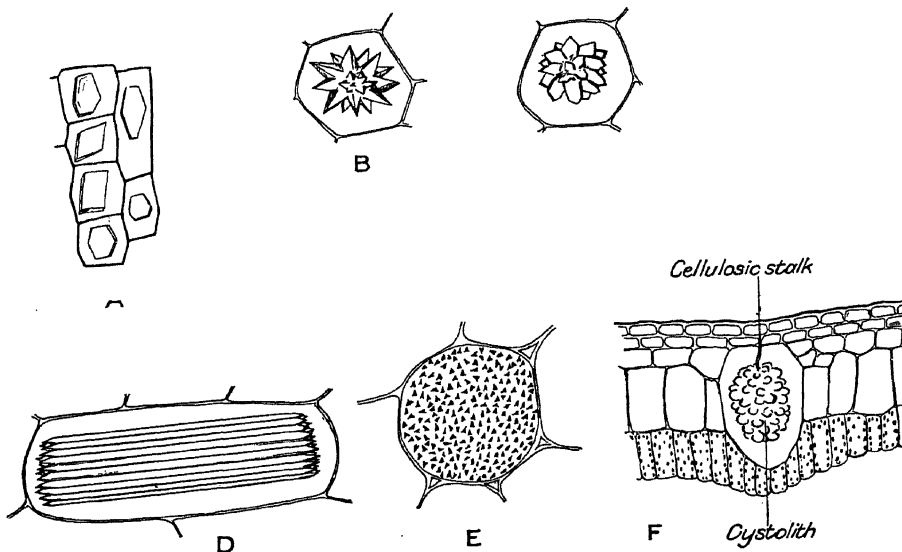


FIG. 23.—Plant Cells containing Crystals.

Calcium oxalate: A, prismatic crystals in *Senna* leaflet; B, cluster-crystal in *Senna* rhizome; C, ditto, in *Rhubarb* rhizome; D, raphides in *Squill* bulb; E, microcrystals in *Atropa Belladonna* root.

Calcium carbonate: F, cystolith in leaf of *Ficus elastica*.

calcium carbonate, sometimes found in plant cells, as this is soluble in both acids with effervescence.

Calcium carbonate is found in its most elaborate form in the leaf of *Ficus elastica*, and the nettle, where it occurs in certain cells as a large nodulated body, or **cystolith**, suspended by a cellulosic thread from the cell wall (Fig. 23, F).

Cell Formation

In the higher plants, the body consists of millions of cells arranged into tissues and organs each of which plays a part in the life of the organism as a whole. The cells of the various tissues of such plants are generally specialised for the work they have to perform.

In the simplest plants, such as *Chlamydomonas*, the organism is but a single cell which must carry out all the vital processes, both vegetative and reproductive. There is no fundamental difference

in structure between such **unicellular** plants, and the individual cells of **multicellular** plants, although differences in behaviour may be apparent.

All multicellular plants start their development as single cells, which will be seen in the various life-histories dealt with in subsequent chapters. By the multiplication of a single cell, and its divisions, an elaborate organism can be formed.

New cells can arise only by the division of pre-existing cells, and cells with the power of division are said to be **meristematic**.

In unicellular plants new cells are formed as a means of reproduction, the cells of one generation dividing to form the next.

Multicellular plants vary in their methods of cell-formation. In the simplest filamentous plants, like *Spirogyra*, each cell of the filament can divide and elongation is brought about along the entire filament. In the thalloid alga, *Fucus* (Fig. 64) the elongation of the thallus is confined to the apices of the branches, where a cell divides repeatedly to leave behind cells which form new tissue.

In the Spermatophyta, the elongation of the axis is carried out, chiefly, by tissues occupying the apices of the stem and root. These **apical meristems**, or **growing-points**, consist of numerous meristematic cells forming cells which are left behind to form permanent tissues, as the apex extends.

The apical meristem is not the only type found in the higher plants, for in the stems of grasses, in addition to an apical meristem, there is an **intercalary meristem** at the base of each internode.

The meristematic cells of all but the simplest plants have thin cellulose walls, prominent nuclei, and non-vacuolated protoplasts, and those of the meristems of the higher plants are compactly arranged without intercellular spaces.

In cell-division it is always found that the nucleus divides first, so that the process is usually referred to as **nuclear-division**. Nuclear division may be **direct** or **indirect**. Direct nuclear division, or **amitosis**, is not of common occurrence, being found in certain simple plants, and occasionally in the mature cells of higher plants (e.g. *Tradescantia* stem) where it does not result in new cell-formation but merely in the presence of more than one nucleus in a cell. It consists in the simple constriction of the nucleus and its subsequent division into two, followed, in some cases, by a division of the cytoplasm to form two cells.

Indirect nuclear division, or **mitosis** (Fig. 24), is found throughout the plant kingdom, and may be studied in the apical meristem of the onion, or other, root. The stages passed through by the nucleus during mitosis have been studied largely in dead stained material, but some of them can be followed in living cells.

In the process, the first changes occur in the chromatin which becomes more prominent (Fig. 24, B) and ultimately forms a coiled thread, the *spireme* (Fig. 24, D) which has a longitudinal groove, and is irregularly coiled around the nucleolus. Later, the nucleolus disappears, and the spireme breaks up into a series of lengths, the *chromosomes* (Fig. 24, E), which, for the vegetative cells of a particular species, are constant in number. Meanwhile, the nuclear membrane has broken down and a *nuclear spindle* of

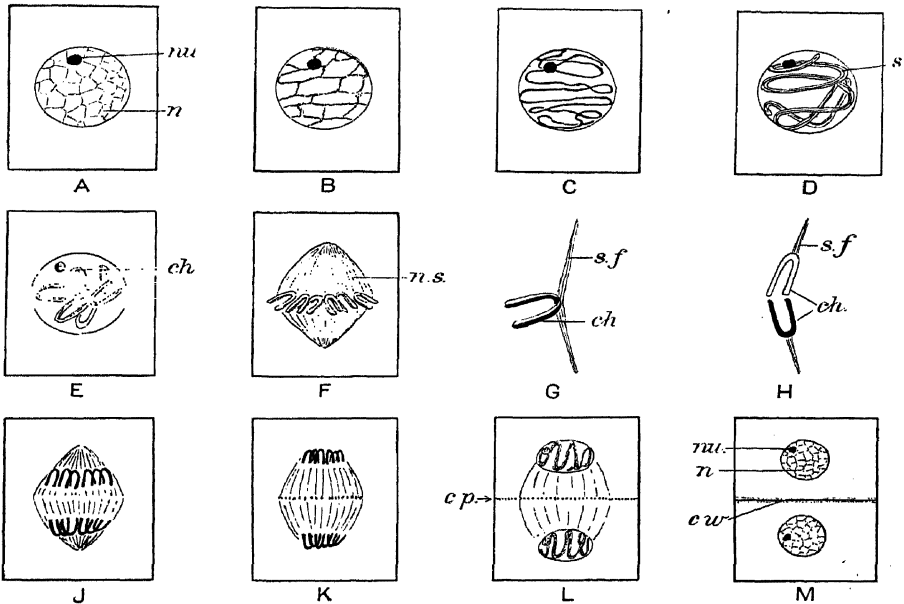


FIG. 24.—Stages in Mitosis of Plant Cell—description in text.

G, chromosome and associated spindle fibres; H, division of chromosome. (ch. = chromosome, c.p. = cell-plate, c.w. = cell-wall, n = nucleus, n.s. = nuclear spindle, nu. = nucleolus, s = spireme, s.f. = spindle fibres.)

fine threads appears, radiating from the opposite *poles* of the nucleus and spreading out towards its centre, or *equator*. The true nature of the spindle fibres is not known, for, although they appear in stained cells, they are not discernible in living cells which show a spindle-like area only. Some authorities believe that they are not true fibres, but represent, in the living cell, channels of flow, differing in colloidal nature from the rest of the protoplasm. The chromosomes, now U or J-shaped, become arranged at the equator of the spindle (Fig. 24, F), and split longitudinally, as indicated by the groove of the previous spireme. The two halves

of each chromosome move to the opposite poles of the spindle (Fig. 24, j), the movement being considered by some to be provided by the contraction of fibres to which the chromosomes are attached (Fig. 24, g, h), and by other authorities to the existence of currents in the cell.

On arrival at the poles (Fig. 24, k) the two sets of half-chromosomes form daughter-nuclei (Fig. 24, l) during which nucleoli appear and new nuclear membranes arise. Whilst this has been proceeding, a thickening of cytoplasm occurs in the equatorial plane of the spindle (Fig. 24, k), and, by a lateral spreading, a cytoplasmic **cell-plate** divides the original cell into two, and isolates the daughter-nuclei (Fig. 24, l). Within this cell-plate, the primary cell-wall is laid down by the protoplasts and consists largely of a carbohydrate, pectose. Later on, by a reaction with mineral substances in the protoplasm, the pectose wall forms a calcium pectate membrane, or **middle lamella**, upon which cellulose is deposited by the protoplasts of the daughter-cells, to form the typical cell-wall (Fig. 24, m).

In the higher plants, during the formation of the cellulose wall following mitosis, the protoplasts are not completely cut off from one another, but remain connected by very fine threads of cytoplasm through the wall. The **protoplasmic continuity** of such tissues is in marked contrast to the condition in lower plants in which the new wall isolates completely the daughter-cells.

Differentiation

The cells, formed by the apical meristems of the higher plants, gradually lose their power of division as they recede from the apex, and become **permanent tissue**. The cells enlarge mainly by the absorption of water, which also causes them to become rounded and partly separated from one another. This separation is due to the rupture of the middle lamellæ at certain points, which results in the formation of small intercellular air-spaces.

As the cells continue to enlarge, small watery vacuoles appear in the cytoplasm and the cell-wall becomes distended. The distension of the wall is made permanent by the deposition of new substance in the wall, such growth of the wall being called **intus-susception**. During the enlargement of the cell the original cytoplasm has not increased in relation to the volume of the cell, so that it finally becomes a peripheral layer enclosing a large vacuole, and presents the appearance described earlier in the chapter. As the enlargement of the cells behind the meristem proceeds, other changes take place which result in their **differentiation** to form the various tissues of the mature plant.

In general the organs of the higher plants are composed of two main types of tissue, viz. *parenchyma* and *prosenchyma*.

Parenchyma is a tissue composed of more or less rounded isodiametric cells and forms a large part of the root, stem, leaf, fruit and seed. Parenchymatous cells characteristically have thin cellulose walls, and are seldom more than twice as deep as they are broad. Examples are found in the cortex and pith of young stems (Fig. 26, B) and in fleshy fruits.

Prosenchyma consists of cells which are much longer than they are broad, and occurs in the conducting and mechanical systems of vascular plants in general. The prosenchymatous cell frequently has tapering ends (Fig. 25, c), so that, as it is forming from a parenchymatous cell of the meristem, its ends must grow between those of other cells, as it elongates.

Some of the most important changes which take place during the differentiation of cells involve the cell-wall, which usually increases in thickness and may become chemically altered. Most of the obvious characters serving to distinguish the various differentiated tissues of vascular plants are those of the cell-wall rather than of the protoplast. During the maturation of a cell, the protoplast adds layers of new substance to the primary wall, generally in some manner typical of the particular tissue to which the cell belongs. This increase in thickness of the wall is called *growth by apposition* in distinction to the increase in area by intussusception previously mentioned. It is uncommon for the deposition of cell-wall material to take place uniformly over the whole wall, although it does occur in some cork cells. The more usual event is for certain parts of the wall to be reinforced whilst the rest remains comparatively thin, giving rise to characteristic elements, according to the plan of deposition. In the pith of the elder stem and certain woody elements of Angiosperms, thin areas called pits are left in the wall which is described as *pitted* (Fig. 29, E, L). A *pit* is not generally a break in the wall, but is covered by the primary wall now known as the *pit-membrane*. In living cells, the protoplasmic connecting threads pass through the walls of the pits, and apparently influence the deposit of wall material, for the wall between two cells is formed by both protoplasts which produce their pits at the same places.

Simple pits have straight sides, whilst *bordered pits*, which occur, for example, in the wood of the pine (Fig. 29, L, M, N) are formed by the overarchings of the surrounding thickened wall, which gives them a typical appearance in surface view.

Other types of thickening of the wall (Fig. 29, F, G, K) consist in the deposit of rings, spirals, or irregular bands resulting in the

formation of *annular*, *spiral* and *reticulate* elements respectively. In the ferns transverse pits occur in the elements of the wood, the thickening of which is called *scalariform* (Fig. 29, J).

In young stems and the larger veins of leaves the walls of certain elongated cells are thickened at the corners with cellulose. This produces a characteristic tissue, *collenchyma* (Fig. 25, A, B) which is the usual mechanical tissue of young or temporary organs. As

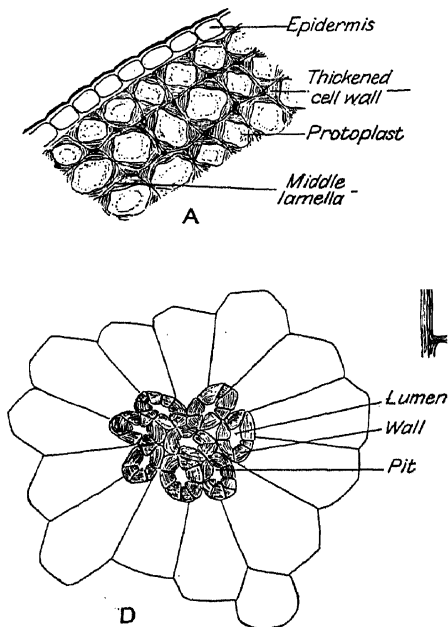


FIG. 25.

A, collenchyma, transverse section; B, ditto, longitudinal section (from stem of Mint); C, single wood fibre; D, group of stone-cells and adjacent parenchyma (from Pear fruit).

seen in transverse section, collenchyma appears to consist of triangular areas of thickening enclosing darker areas which are the protoplasts of the cells. Collenchymatous cells are found particularly in young stems undergoing elongation. This is owing to the fact, that as the cellulosic cell-wall permits the ready entry of watery solutions and nutrient materials, the protoplast remains alive and continues the growth of the cell. Thus, whilst the thick walls strengthen the organ, the tissue does not interfere with its elongation. Collenchymatous cells have blunt ends (Fig. 25, B),

and when near the surface of an aerial organ, their protoplasts may contain chloroplasts.

It is uncommon for pure cellulose to be laid down during the growth by apposition of cell-walls. It is more often the case that other substances are deposited, either to replace cellulose or to accompany it. As a cell grows older its wall may alter chemically, which may alter, also, the physical properties of the wall.

In the epidermis of leaves and young stems exposed to the atmosphere, the outer walls of the cells are thickened with *cutin*, a complex mixture of substances of fatty nature. The cutin is formed by the protoplast, impregnates the wall and accumulates at the surface as a varnish-like layer, the *cuticle* (Fig. 43, B). Cutinised walls are almost impervious to water and form a suitable protection against excessive water-loss in those organs exposed to drying influences.

Somewhat similar to cutin is *suberin*, which is deposited in the walls of cells constituting cork. Suberin, like cutin, contains fatty substances, and stains red with an alcoholic solution of the stain Sudan III. Cork cells are found in the bark of woody organs, being compactly arranged without intercellular spaces. Suberised walls are extremely impervious to water and relatively impervious to gases; they are unpitted. They play the same part in woody organs as cutinised walls play in young organs, in preventing water-loss. As suberisation usually involves the whole of the cell-walls, the protoplasts are cut off from nourishment, and die as differentiation is completed.

In the formation of the woody tissues of plants the cell-wall becomes thickened with *lignocellulose* which consists of an altered form of cellulose together with a complex material *lignin*. Lignified walls are stronger and not so extensible as pure cellulose walls, and thus give mechanical strength of a more permanent type than is found with collenchymatous cells. For this reason the mechanical tissues of older organs consist of special lignified cells which form a tissue called *sclerenchyma*. Sclerenchymatous elements may be either parenchymatous or prosenchymatous. In the former case the cells, known as *stone cells*, are rounded and have thick lignified walls penetrated by deep pits (Fig. 25, D). The best examples of stone cells are found in the woody shell of the coconut and in the plum stone, both of which are composed of closely packed stone cells forming a protection for the enclosed seed. Groups of stone cells are found in the fleshy pulp of the pear fruit which owes its gritty nature to their presence.

The elongated sclerenchymatous cell is called a *fibre* which has thickened walls with few pits and long tapering ends (Fig. 25, C).

Lignified fibres have great tensile strength and can undergo considerable stretching without losing their power of recovery. They occur in the wood and other tissues of Angiosperms where mechanical strains, such as bending and stretching, are encountered. As the lignification of a cell-wall proceeds, it is usual for the protoplast to die. The reason for this is not understood, for lignified walls are to some extent permeable to watery solutions. In the lignified dead cell the space formerly occupied by the protoplast and vacuole is called the *lumen*, which may be occupied by water or gas according to the type of element.

The death of the protoplast of lignified cells does not mean that the cell loses its utility, for, apart from the strength afforded by the walls, the lumina of the lignified cells in the wood of plant organs are the path along which water and dissolved substances are rapidly conducted through the plant. These lignified conducting elements, known as *vessels* and *tracheids*, will be considered in the next chapter.

Lignified walls are distinguished by their reactions. They stain red with an alcoholic solution of phloroglucin followed by hydrochloric acid, and yellow with aniline chloride or sulphate. Like cutin and suberin, lignin is insoluble in cuprammonia.

CHAPTER VI

THE ANATOMY OF ANGIOSPERMS

The organs of both herbaceous and woody Angiosperms are composed of tissues arranged in some particular manner according to the organ. The arrangement of the fundamental tissues is so characteristic that it provides a means of identification of an organ, and, in some cases, of the group of plants.

The structure of herbaceous Angiosperms is simpler than that of woody forms, although the latter plants are essentially herbaceous in their early stages, and present the usual anatomical features of such plants.

The arrangement of the tissues of a plant organ may be conveniently studied by means of a transverse section, but it should be remembered that, in order to ascertain the nature of the component cells, longitudinal sections may also be necessary.

The Stem

(a) **Herbaceous Dicotyledon Stem.** The structure of a young herbaceous Dicotyledon stem may be studied in an upper internode of the Californian poppy (*Eschscholtzia*). The transverse section (Fig. 26, A) is round, or somewhat angular, in outline, and consists of an outer layer, the *epidermis* enclosing parenchymatous tissue. Situated in the parenchyma, some distance from the epidermis, is an interrupted ring of *vascular bundles* which divides the parenchyma into an outer *cortex* and a central *pith* or *medulla*. Between the bundles are broad bands of parenchyma, the *primary medullary rays*.

The arrangement of the vascular bundles, which form the conducting system of the organ, into a ring is characteristic of nearly all Dicotyledon stems. If the tissues are examined in detail (Fig. 26, B) it will be seen that the epidermis consists of small cells, the outer walls of which are cutinised. The cells are living, but have few features of importance, and several of them may be prolonged outwards to form hairs. Here and there the epidermis is penetrated by pores or *stomata*, which are formed by special pairs of epidermal cells containing chloroplasts. Beneath the epidermis are groups of collenchyma, occurring in the stem as longitudinal

strands, and between these are parenchymatous cortical cells containing chloroplasts.

Numerous small intercellular spaces are present in the cortex, serving to provide an aerating system which is in communication with the atmosphere by way of the stomata. The cortex is delimited on the inside by a continuous ring of small cells, not very clearly defined in this stem but more obvious in that of the Michaelmas daisy. These cells contain minute starch grains and form the *endodermis*, sometimes called the *starch-sheath*.

All the tissues within the endodermis constitute the *stele*. The outermost layer of the stele, immediately within the endodermis,

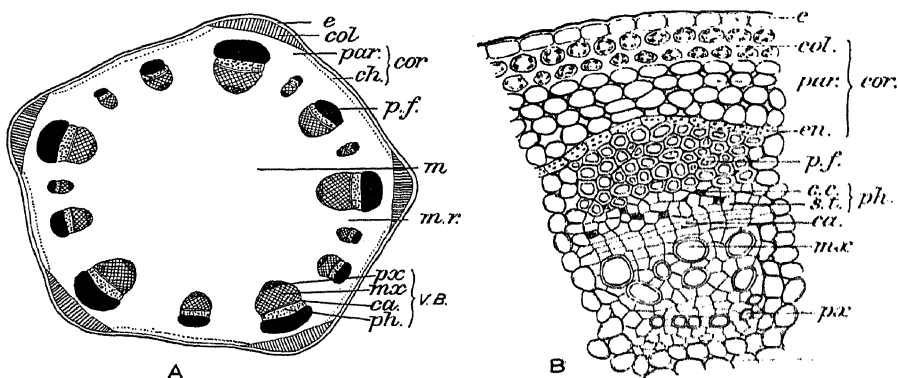


FIG. 26.—Transverse section of young stem of Californian Poppy (*Eschscholtzia*).

A, plan of tissues; B, part of section, in detail.

(ca. = cambium, c.c. = companion cell, ch. = chlorenchyma, col. = collenchyma, cor. = cortex, e = epidermis, en. = endodermis, m. = medulla, m.r. = primary medullary ray, mx. = metaxylem, par. = cortical parenchyma, p.f. = pericyclic fibres, ph. = phloem, px. = protoxylem, s.t. = sieve-tube, V.B. = vascular bundle.)

is the *pericycle*. The pericycle consists of groups of lignified fibres opposite to each vascular bundle, and between the groups of fibres pericyclic parenchyma occurs. Each vascular bundle is composed of three tissues, which are the *phloem*, outermost, the *xylem* or wood, innermost, and between them, a thin strip, the *cambium*. The pith consists of large rounded parenchymatous cells, which, in lower internodes, may enclose a central cavity due to the rupture of its cells.

Before describing the details of the vascular tissues, their origin from the apical meristem must be considered. The extreme apex of the stem is occupied by the *primordial meristem* (Fig. 27) which gives rise to all the tissues occurring below. It consists of the usual isodiametric meristematic cells compactly arranged.

PLATE I

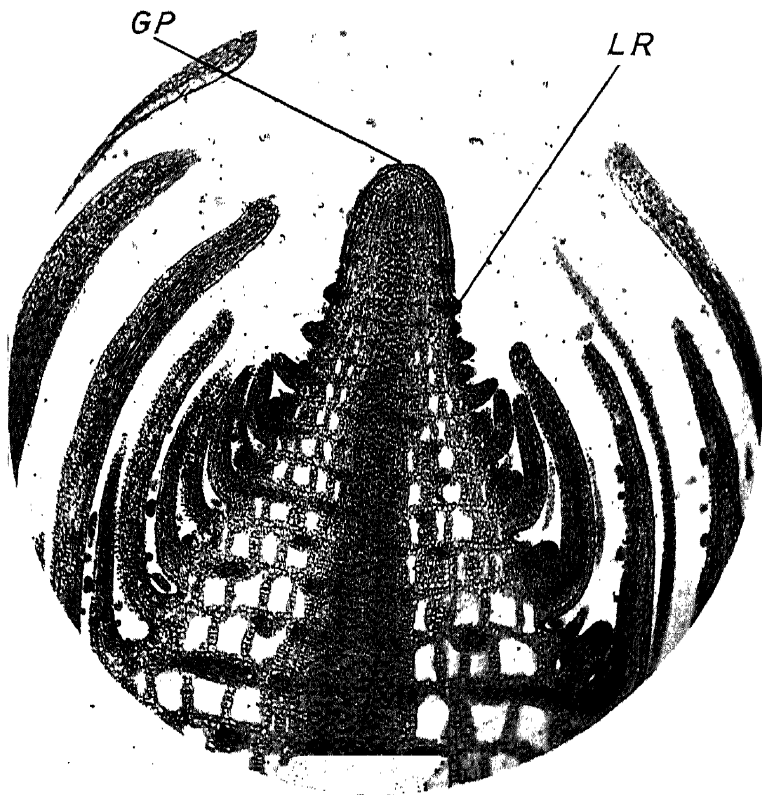


FIG. 27.—Longitudinal section of the stem apex of *Hippuris*, showing the primordial meristem (*GP*) and the exogenous origin of the leaves, as lateral outgrowths (*LR*) of the stem. The older leaves have developed axillary buds.

As the cells formed by this meristem enlarge they cause its continual advance, and as they differentiate form the tissues of the mature stem. The tissues encountered in passing backwards from the apex must be progressively older, and thus display the manner in which the various permanent tissues of the organ have been produced.

Immediately behind the primordial meristem, the cells, which are still meristematic, have become defined as three layers or *histogens* (Fig. 27), viz. the *dermatogen*, the *periblem*, and the *plerome*. The dermatogen is outermost and forms cells which differentiate to become the epidermis. Within the dermatogen is the periblem, which, by the division of its cells in several planes, produces the cortex, and in the centre is the plerome which gives rise to the whole of the stele. An important part of the plerome is the *procambium* which in the Dicotyledon stem takes the form of a ring of *procambial strands* arranged in a manner like that of the vascular bundles which they ultimately produce. The procambial cells are elongated slightly, and divide by walls parallel to the surface of the stem to cut off cells both to the inside and to the outside. Those cells cut off to the outside, differentiate to form the phloem and those to the inside become the xylem, whilst a central part of the strand retains its meristematic properties to survive as the cambium of the vascular bundle. The formation of xylem and phloem is progressive, the young bundle, near the apex of the stem, possessing smaller amounts of these tissues than an older bundle lower down the stem. The first-formed vascular tissues are known as *protoxylem* and *protophloem*, which differ from the later tissues which are added to them. The later-formed xylem, or *metaxylem*, arises to the outside of the protoxylem which is therefore the innermost part of the vascular bundle, and the later-formed phloem, or *metaphloem* arises to the inside of the protophloem. It is in this way that the *primary* vascular bundle is produced, consisting of protoxylem, metaxylem, cambium, metaphloem and protophloem in that order from the centre of the stem. A vascular bundle of this type in which the xylem and phloem occupy the same radius is said to be *collateral*, and because it possesses a cambium it is described as *open*. Open collateral vascular bundles are found only in the stems of Dicotyledons and Gymnosperms. The elements of the tissues of the Dicotyledon bundle are, however, characteristic of Angiosperm plants only.

The phloem consists largely of elongated structures of two kinds, viz. *sieve-tubes* and *companion cells*. A sieve-tube (Fig. 28) is a longitudinal row of cells whose protoplasts have lost their nuclei and become disorganised in the centre to form a slimy

material. Their walls are composed of cellulose, but the pit-membranes of their pitted end-walls have disappeared to permit of the communication of adjacent protoplasts by broad slimy strands. The perforated end-walls usually become thickened around the pits with a carbohydrate, callose, and appear in surface view (Fig. 28, B) as the so-called *sieve-plates*. The sieve-tube is the

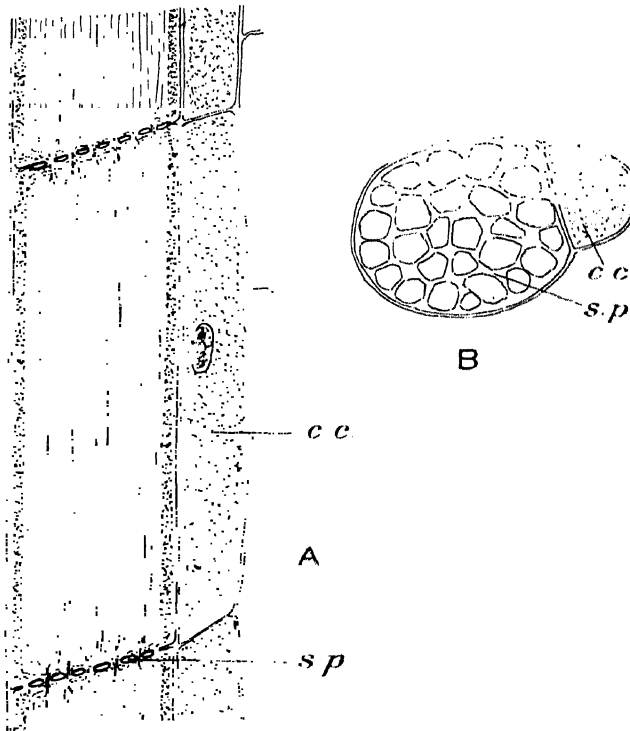


FIG. 28.—Sieve-Tube with Companion Cell.
A, longitudinal section; B, transverse section.
(c.c. = companion cell, s.p. = sieve-plate.)

main channel for the passage of elaborated food material through the plant, rapid transport being assisted by the continuity of the protoplasts. The companion cell is found in Angiosperms only, and is a cell with thin cellulose walls, dense protoplast and prominent nucleus, closely associated with a sieve-tube. It is formed by the same mother-cell as the adjacent sieve-tube cell, having arisen by division after the mother-cell was cut off by the procambium or

cambium. Besides sieve-tubes and companion cells, the phloem contains parenchymatous cells, and in some plants, though not in the Californian poppy, sclerenchymatous fibres may be present amongst the other elements.

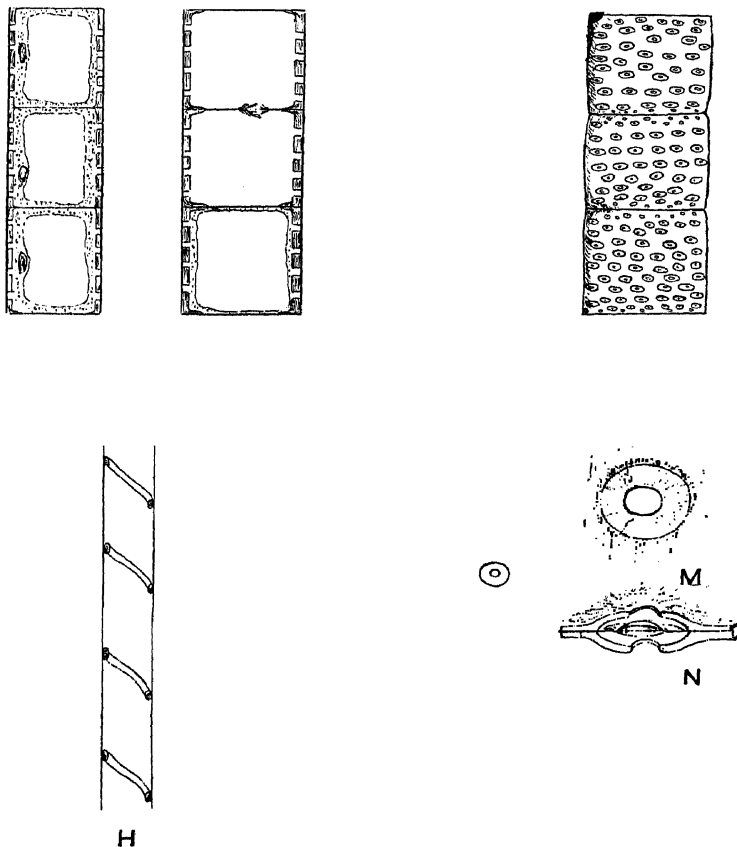


FIG. 29.

A-E, development of Vessel (description in text); E-L, various types of thickening of Vessels and Tracheids; E, pitted; F, annular; G, spiral; H, ditto, sectional appearance; J, scalariform; K, reticulate; L, bordered pits in Gymnosperm tracheid; M, single pit of L; N, section of same.

The xylem consists of a number of different elements, the most characteristic of which is the *vessel*. A vessel, like the sieve-tube, is formed by a vertical row of slightly elongated cells (Fig. 29, A), which arises from the procambium. The longitudinal walls become

lignified, the protoplasts of the cells die, and the intervening end-walls break down to result in the formation of a tubular structure whose cavity or lumen contains water (Fig. 29, D). The vessels of the xylem are the main channels through which water and dissolved substances pass upwards through the plant. The thickening of the walls of the vessel varies in character. In the protoxylem it is either annular or spiral, as such thickening does not interfere with the stretching of the vessel necessitated by it occurring in that part of the stem which is still undergoing elongation. The vessels of the metaxylem are usually pitted or reticulate, the greater thickening of the wall being permissible as this tissue arises in that part of the stem which has generally completed its elongation. The xylem of the Californian poppy stem consists of vessels and living wood parenchyma. In other stems, especially those which will later become woody, another type of lignified conducting element may be present as well as the vessels. This is the *tracheid* which resembles a vessel in the nature of its wall but differs in that it is a single elongated cell with oblique pitted ends. In some herbaceous stems, and characteristically in those of woody Dicotyledons, the xylem includes a proportion of thick-walled wood fibres, which strengthen the tissue.

In annual herbaceous stems the cambium is not well defined, and, in fact, towards the end of the growing season may differentiate to form permanent tissue. The details of its structure will be considered when describing the woody stem, in which it is an important tissue (p. 60).

Although the typical Dicotyledons have a primary stem structure of the type described, the members of certain families exhibit a slightly different arrangement. In the families Cucurbitaceæ (e.g. vegetable marrow), Solanaceæ (e.g. *Atropa Belladonna*), Myrtaceæ (e.g. *Eucalyptus*), Apocynaceæ (e.g. periwinkle) and a few others, the vascular bundles possess an additional phloem to the inside of the protoxylem. Such bundles are *bicollateral*, and are exemplified by those of the vegetable marrow, which incidentally provide excellent examples of sieve-tubes and vessels. A transverse section of the vegetable marrow stem (Fig. 30) is pentagonal in outline, owing to the ridged stem. Following the contour of the section is a ring of vascular bundles dividing up the ground tissue, as in the Californian poppy. The outer tissues are very similar to those of the Californian poppy stem, except that in this case the feebly-thickened pericyclic fibres form a complete ring, within which is a continuous zone of pericyclic parenchyma. The vascular bundle consists of external phloem, cambium, xylem, and internal phloem, the two phloem groups being of similar structure.

The protoxylem of the primary xylem, like that of the typical collateral vascular bundle, is innermost and described as *endarch*.

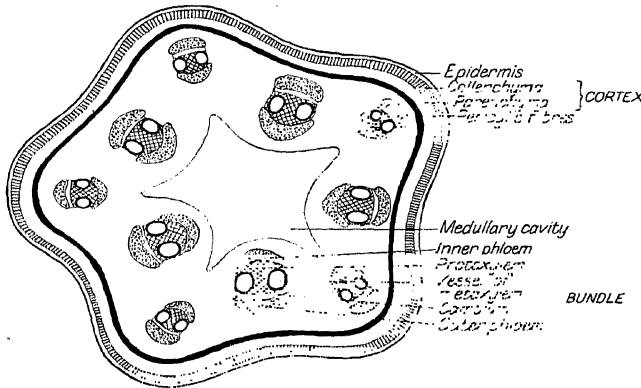


FIG. 30.—Plan of tissues in transverse section of stem of Vegetable Marrow (*Cucurbita*).

(*b*) **Monocotyledon Stem.** The great majority of Monocotyledon stems are herbaceous and their typical structure can be seen in the internode of the maize (Fig. 31, A). A transverse section of

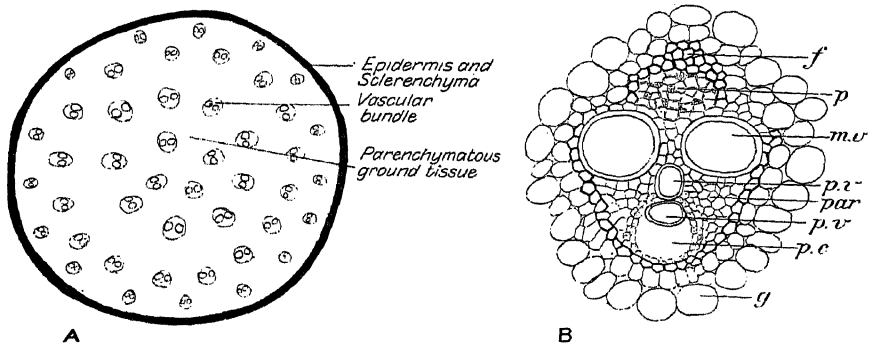


FIG. 31.—Transverse section of stem of Maize (*Zea mays*).

A, plan of tissues; B, vascular bundle in detail.

(*f* = fibrous bundle-sheath, *g* = ground tissue, *m.v.* = metaxylem, *p* = phloem, *par.* = xylem parenchyma, *p.c.* = protoxylem canal, *p.v.* = protoxylem vessel.)

this stem shows a very different arrangement to that of the Dicotyledon. The vascular bundles are more numerous and appear to be scattered irregularly throughout the parenchymatous ground tissue, but are actually arranged in a series of concentric rings.

The differentiation of the ground tissue into cortex and medulla

is not feasible in this stem, although in some Monocotyledons such as the orchid, *Cypripedium*, a parenchymatous cortex and sclerenchymatous pericycle can be distinguished. The vascular bundle (Fig. 31, B) consists of xylem and phloem only, the whole of the original procambial strand having been used up in the formation of the primary tissues. This type of vascular bundle, devoid of a cambium, is described as *closed*, but, like that of the Californian poppy, it is collateral and has an endarch protoxylem. The xylem is roughly V-shaped, the apex being occupied by the protoxylem which consists of an annular vessel and a spiral vessel, and a small amount of parenchyma. The bulk of the protoxylem parenchyma, and occasionally some of the vessels also, break down to form a *protoxylem canal*. The metaxylem is composed of two prominent pitted vessels, some small tracheids and parenchyma. The phloem, lying within the large vessels of the metaxylem, possesses sieve-tubes and companion cells only. The ground tissue immediately surrounding the bundle is sclerenchymatous and forms a strengthening *bundle-sheath* which is usually wider on the outer side. Sclerenchyma also occurs beneath the cutinised epidermis.

(c) **Woody Dicotyledon Stem.** In woody Dicotyledons the persistent aerial stem increases in size year by year, adding new branches when the buds develop in the spring, and growing in

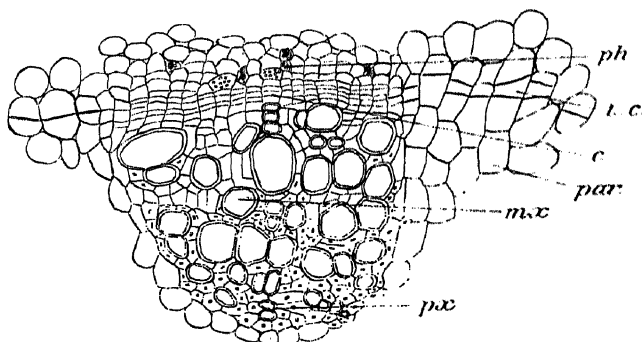


FIG. 32.—Part of transverse section of stem of *Aristolochia*, showing a vascular bundle, and origin of interfascicular cambium in adjacent medullary rays. (c = fascicular cambial zone, i. c. = interfascicular cambial cell, mx. = metaxylem, par. = parenchyma of medullary ray, ph. = phloem, px. = protoxylem.)

thickness throughout its life. The increased girth is mainly due to the addition of new vascular tissue, this being required to provide the conducting system for the increasing foliage, and the mechanical support for the more extensive branching.

In the early stages of its growth, the stem of a woody Dicotyledon

has a similar structure to that of a herbaceous stem, but during the first season changes take place. In many cases, such as in *Aristolochia*, a woody climbing plant, the stem, when a few weeks

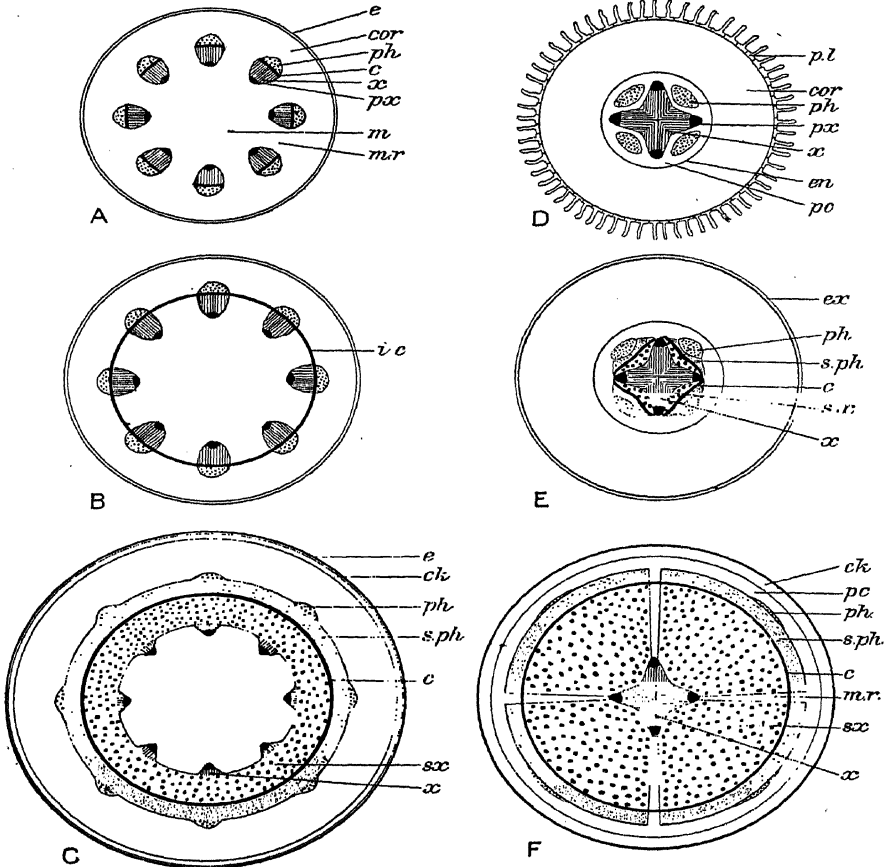


FIG. 33.—Diagrams to show secondary growth in a Dicotyledon plant.

A–C, Stem; D–F, Root.

(c = cambium, ck. = cork, cor. = cortex, e = epidermis, en. = endodermis, ex. = exodermis, i.c. = interfascicular cambium, m. = medulla, m.r. = primary medullary ray, p.c. = pericycle, ph. = primary phloem, p.l. = piliferous layer, px. = protoxylem, s.ph. = secondary phloem, s.x. = secondary xylem, x = primary xylem.)

old, has a ring of open collateral vascular bundles. Later in the year certain cells of each parenchymatous medullary ray become meristematic, and divide by tangential walls to form an additional cambium, called the *interfascicular cambium* (Fig. 32), to dis-

tinguish it from the *fascicular cambium* of the primary bundles. This new cambium unites with that of the bundles and, like the fascicular cambium, cuts off phloem to the outside and xylem to the inside. In this way a complete ring of vascular tissue, consisting of phloem, cambium and xylem, is produced by the end of the first year (Fig. 33, c).

In some woody plants, interfascicular growth results in the insertion of complete *secondary vascular bundles* between the primary bundles, but by the end of the first season a condition similar to that produced by the formation of interfascicular cambial strips, is arrived at. The behaviour of the cambial cells is characteristic.

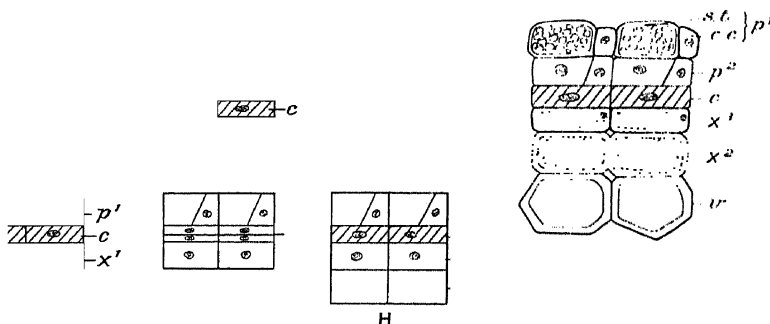


FIG. 34

A, two cambial cells; B-J, diagrammatic representation of origin of vascular tissues from cambium.

(c = cambial cell, c' = division of cambial cell, c.c. = companion cell, p¹ and p² = cells to form phloem, s.t. = sieve-tube, v = vessel formed from X¹, X², X³ and X⁴ = cells to form xylem.)

Each cell divides tangentially to form two daughter-cells, one of which remains meristematic as a cambial cell, whilst the other differentiates to form either xylem or phloem (Fig. 34). The reasons for the differentiation are not at present known, and all that can be said is, that if the outer cell differentiates it forms phloem, but if the inner cell differentiates it becomes xylem. The differentiating cell may form any one of the characteristic elements of the tissue to which it is added, except in the phloem, when the cell, before differentiating, may undergo one further division to give rise to a sieve-tube cell and its associated companion cell (Fig. 34, J).

Those cambial cells producing conducting tissues are longer than they are broad, and have either oblique tapering (Fig. 34, A), or chisel-like ends. Part of the cambial ring consists of smaller cells, which, in longitudinal view, appear as spindle-like groups. These

cells divide to form radial strips of parenchymatous tissue to each side of the cambium, forming the **medullary** or **vascular rays**. Each ray consists of elongated cells running across the xylem and phloem and provides a path for the lateral transport of solutions in the stele. Vascular rays may be the site of stored food, accumulating in the late growing season starch, which is drawn on by the

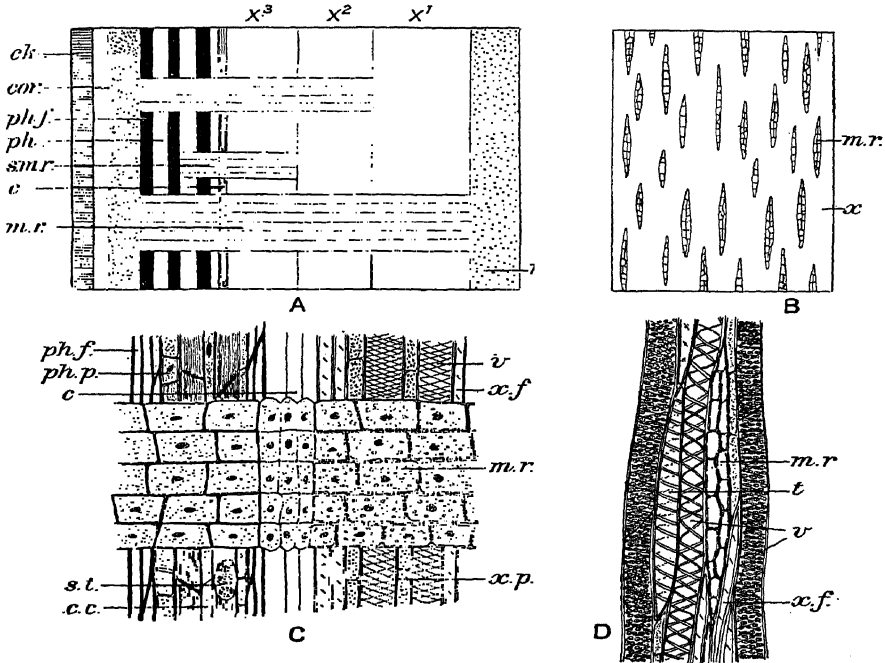


FIG. 35.—Longitudinal sections of Woody Stem of Lime (*Tilia*).

A, plan of tissues in radial L.S.; B, plan of tissues of tangential L.S. of xylem;
C, part of A, in detail; D, part of B, in detail.

(c = cambium, c.c. = companion cell, ck. = cork, cor. = cortex, m. = medulla, m.r. = primary medullary ray, ph. = phloem, ph.f. = phloem fibres, ph.p. = phloem parenchyma, s.m.r. = secondary medullary ray, s.t. = sieve-tube, t. = tracheid, v. = vessel, x. = xylem, x¹, x², x³ = 1st, 2nd, and 3rd year's xylem, x.f. = wood fibre, x.p. = xylem parenchyma.)

buds in the following spring. Medullary rays are not continuous down the stem but are in the nature of radial wedges driven into the conducting tissues (Fig. 35).

The cambium of a one-year old stem remains inactive during the late autumn and winter, but resumes division in the following spring. At the beginning of the second year it behaves in the same way as previously, adding new xylem and phloem to the tissues already present. The amounts of xylem and phloem formed are unequal,

and, as a rule, about four times as much xylem as phloem is added in one year.

The cambium survives throughout the remaining life of the stem, which may be for many years, continuing to form additional tissue in its characteristic manner.

The tissues added to an organ after it acquires its primary structure are described as *secondary*. Secondary xylem consists mainly of pitted vessels, but also a proportion of tracheids, fibres and parenchyma, according to the species. The tissue is characteristically composed of lignified cells, and is comparatively incompressible, so that, as the stem grows older, a large woody cylinder is formed. Secondary phloem is composed largely of cells with cellulose walls, and is not a strong tissue. Consequently, when the volume of wood increases, pressure is exerted on the outer tissues, which results finally in the crushing and death of the outermost phloem elements. As the compression of the outer, older phloem and its resultant death are progressive year by year, the amount of secondary phloem in an old stem is small compared with the wood. As a rule, the only functional phloem in a woody stem is that of the current year and sometimes also that of the year immediately previous.

During the growth in thickness of the stem it is obvious that the cambial ring must have increased its circumference. The increase in circumference is accomplished by a small amount of lateral stretching of the cells, but largely by their radial division. When a cambial cell divides radially both daughter-cells remain meristematic, and after enlarging to the mature size divide tangentially in the usual manner. The secondary xylem formed in each season consists of two zones (Fig. 36, B). There is an inner zone of coarse texture consisting of thin-walled vessels with large lumina, and an outer zone of finer texture composed of narrow vessels and a proportion of fibres or fibrous-tracheids. The coarse *spring-wood* is formed at the time that the buds are opening and its vessels provide a path for the rapid transport of water to the delicate leaves. The finer *summer* (or *autumn*) *wood* is added when the leaves are mature and have a more efficient epidermis, and the demand for water is not so great, and although the tissue is conductive it chiefly provides mechanical strength. In an old stem, the contrasting spring and summer wood gives rise to the so-called *annual rings* (Fig. 36, A), from which the age of the stem may be approximately calculated. It sometimes happens, however, that a tree may become defoliated before the autumn by adverse conditions or insect larvæ. This causes the development of dormant buds which form new leaves, so stimulating the cambium to produce, for the second time that season, wood of the spring type.

The woody cylinder of many old Dicotyledon stems possesses a central xylem of darker colour than the young outer xylem. The dark-coloured **heart-wood** has lost its conducting powers and owes its colour to the deposit of by-products, such as oils, resins, tannins and gums, in its walls or lumina, the conduction of water being carried out by the light-coloured **sap-wood** only. Generally the

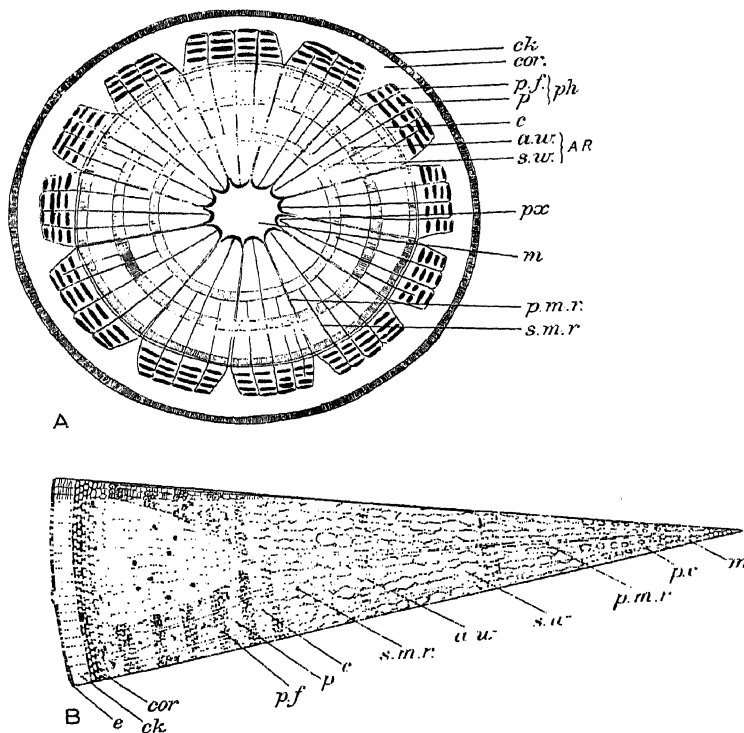


FIG. 36.

A, diagram of transverse section of three-year-old woody stem of Lime (*Tilia*);

B, part of A, in detail.

(A.R. = annual ring, a.w. = summer wood, c = cambium, ck = cork, cor = cortex, e = epidermis, m = medulla, p = soft bast, p.f. = hard bast, ph = phloem, p.m.r. = primary medullary ray, px = protoxylem, s.m.r. = secondary medullary ray, s.w. = spring wood.)

heart-wood is more durable than the sap-wood, and in oak, walnut, ebony and teak provides the timber of commerce. As the sap-wood is the path of water-conduction it is possible for the heart-wood to decay without causing the death of the shoot. This is a common happening in ancient oak trees and other plants, which thrive despite their hollow stems.

It is evident that when the stele of a woody stem increases in diameter some changes must occur in the outer dermal system at the same time. The epidermis of the original stem is a comparatively inextensible tissue, and must, sooner or later, be broken by the pressure from within. If this were to occur without other changes, the exposure of the inner tissues would be a source of danger to the plant, both on account of the loss of water and the liability to infection by fungi and bacteria. To prevent these possibilities the epidermis is usually replaced in the first season by

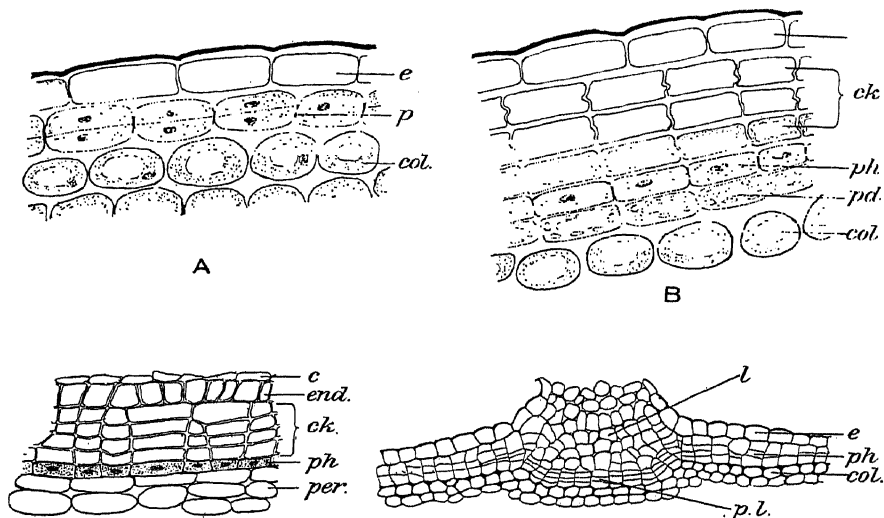


FIG. 37.—Cork formation (transverse sections).

A, B, first-year stem of Elder ; C, woody root of Poplar ; D, lenticel in stem of Elder.

(*c* = remains of cortical parenchyma, *ck*. = cork, *col*. = cortical collenchyma, *e* = epidermis, *end*. = endodermis, *l* = loose parenchyma of lenticel, *p* = hypodermis forming phellogen, *pd*. = phelloderm, *per*. = pericycle parenchyma, *ph*. = phellogen, *p.l.* = phellogen of lenticel.)

a stronger tissue, the cork, which is regenerated to permit of an increased growth in circumference as the stem grows older. In a large number of trees, including the oak, elm and elder, the replacement of the epidermis commences with meristematic activity in the layer of cortical cells immediately below (*hypodermis*). The hypodermal cells divide by tangential walls (Fig. 37, A) cutting off to the outside, cells whose walls become suberised and form cork (Fig. 37, B). This meristem is called the **phellogen**, and because it behaves somewhat like the cambium of the stele, is also known as the **cork-cambium**. The outer cells, originating from the

phellogen, are arranged in regular radial rows without intervening intercellular spaces, and their walls are unpitted. Owing to the deposit of suberin the protoplasts of cork cells die and the lumina are filled with air or other gas. Cork forms a very suitable outer tissue for a persistent aerial organ. The suberised walls prevent water-loss, and the presence of air in the lumina of the cells causes the tissue to be a bad conductor of heat, so guarding the plant against the effects of low external temperatures. The walls, and occasionally the lumina of cork cells, may have tannins, resins and other substances deposited in them, and such substances may protect the inner tissues from the deprivations of insects.

In addition to forming cork cells, the phellogen may, as in the elder, cut off cells to the inside. These cells remain living, and their walls unsuberised, producing a thin zone of tissue, the *phellogen* or *secondary cortex*.

In the stems of the apple and willow, the phellogen is formed by the epidermis itself, whilst in the barberry and currant it arises much deeper in the cortex than in the elder. In all cases where the phellogen arises below the epidermis, any tissues outside the cork layers are deprived of nourishment and die to form the outer part of the *bark*. The term 'bark,' used botanically, refers to the tissues external to the phellogen, but employed in drug descriptions it includes all tissues external to the true cambium. In such drug barks as cinnamon and *Quillaria* the corky bark is, in fact, removed before the drug is placed on the market.

Apart from the tissues it forms, the phellogen differs from the stelar cambium in another important respect. It is uncommon for the first phellogen to survive throughout the entire life of an organ. In the oak, elm and walnut, for example, the primary phellogen continues its activity for several years, but it ultimately differentiates and is replaced by a deeper-seated secondary phellogen. During the life of such plants, numerous phellogens are produced, and it is largely by this means that the increased circumference, necessitated by the enlarging vascular tissue, is brought about. In the beech, the first phellogen remains throughout and is not replaced, which results in the formation of a much smoother bark than is found in stems with numerous phellogens.

Owing to the impervious nature of cork, were it to form a complete covering over the entire stem, the living tissues inside would experience some difficulty in carrying out respiration. It is found that when cork is being formed special pores occur, which are the *lenticels* providing for gaseous exchanges. Lenticels are produced by a special development of the phellogen beneath some of the stomata of the original epidermis. At these points, instead of

forming cork cells, the phellogen gives rise to an unsuberised tissue, the cells of which become rounded to form a powdery tissue, through which gases can readily pass (Fig. 37, D). As water-loss may take place through the lenticel, in some trees it is sealed up in the winter by a thin layer of cork which is broken in the next spring by the formation of more powdery tissue.

Secondary growth does not occur in the vast majority of Monocotyledon stems, even of tree-like form such as the palms. The stem may increase in thickness for a time by the enlargement of cells of the primary tissues. In a very limited number of Monocotyledons, secondary growth takes place in the stem, but in a different manner from that in Dicotyledons. In *Dracæna*, and a few others, with primary stem structure similar to that of the maize, secondary tissues are formed in the parenchyma immediately outside the outermost ring of vascular bundles. The cells of this zone become meristematic and form groups of cells which become new closed bundles, and cells which form the additional ground tissue around the bundles (Fig. 38). This development causes an increasing thickness of the stem, but does not produce the large woody cylinder characteristic of the Dicotyledon stem. A certain degree of woodiness may result from the lignification of the ground tissue, but this, of course, has only a mechanical function.

The Root

The internal structure of the root shows little variation amongst the groups of vascular plants. It does, however, always contrast with the stem structure of the same plant.

Roots are characterised by a small central stele surrounded by a wide cortex, the xylem serving not only for conduction but providing the mechanical resistance to the pulling strains usually experienced by the root. The apex of the root is occupied by a primordial meristem like that of the stem. This produces the same histogens, but, in addition, there is a fourth layer, the *calyptragen*, which overlies the dermatogen at the extreme apex of the root (Fig. 39). The histogens of the root form the same general tissues as those of the stem, the procambium of the plerome arising as a single central strand. The calyptragen cuts off cells which differentiate to the outside and die to become the *root-cap*. As the outer cells of the root-cap are worn away by the growth of the root through the soil, they are replaced from within by the calyptragen. The protection of the apex of a root by dead tissue contrasts with that of the stem, provided, as a rule, by overlapping young leaves.

(d) **Herbaceous Dicotyledon Root.** The adventitious root of the buttercup is a typical example of the primary Dicotyledon root,

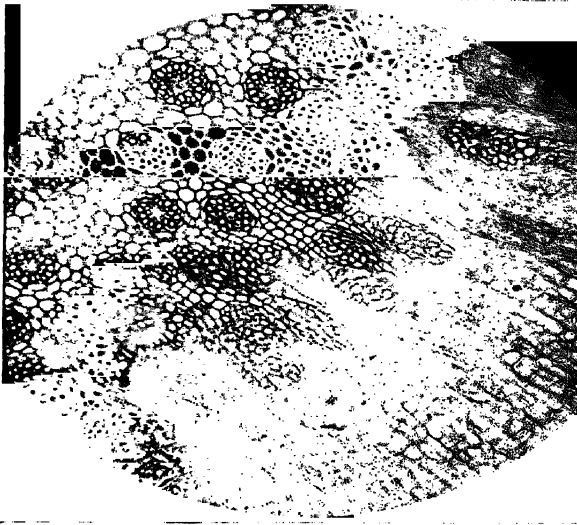


FIG. 38.—Photomicrograph of part of a transverse section of the stem of *Dracæna*, showing the development of secondary bundles, to the right of the picture.

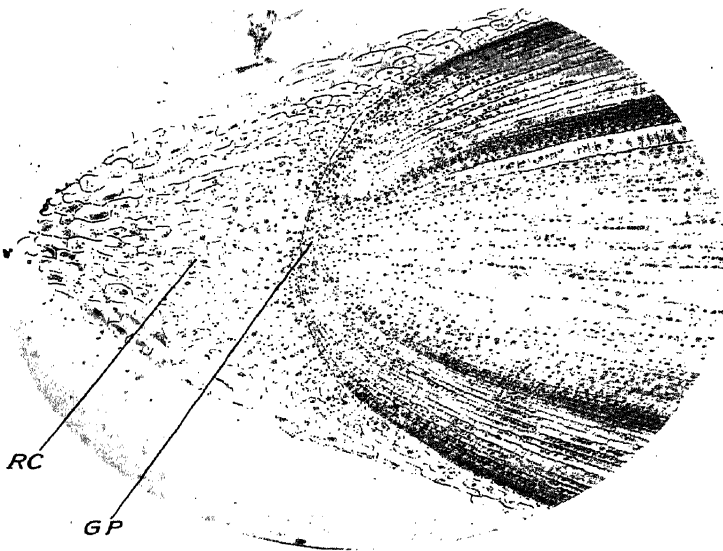


FIG. 39.—Longitudinal section of the root-tip of *Zea* (Maize), showing the apical meristem (*GP*) and the root-cap (*RC*).

for, although originating in a different manner from the tap root of the broad bean, exhibits the same general zones. The various regions of the root display slightly different anatomical structure, but the characteristic arrangement of the tissues of a young root can be seen in a transverse section through the absorptive region bearing the root-hairs (Fig. 40). The outermost tissue of the root is a single layer of cells, the **piliferous layer**, many of the cells of which are elongated beyond the surface as **root-hairs**. Within the piliferous layer is a broad parenchymatous cortex delimited on the

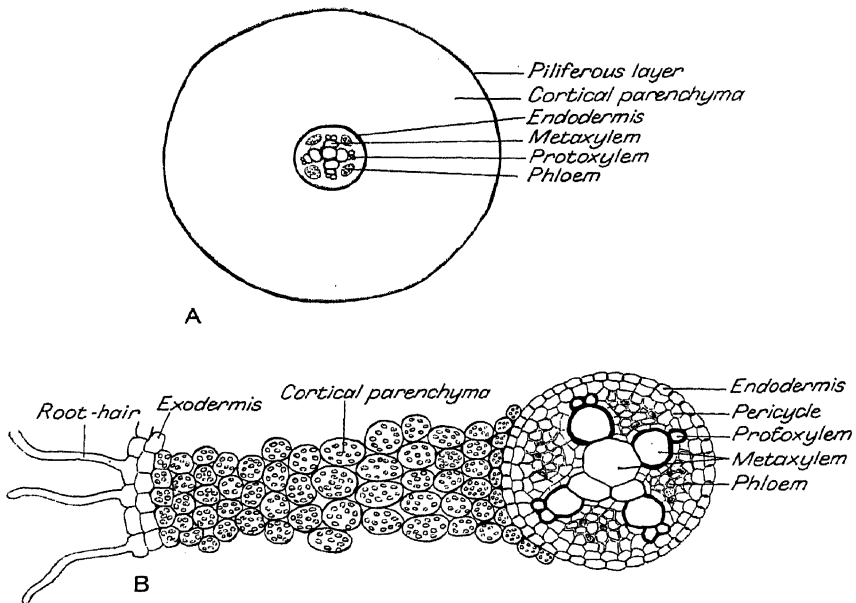


FIG. 40.—Transverse section of root of Buttercup (*Ranunculus repens*).
A, plan of tissues; B, part of A in detail.

inside by an endodermis which surrounds the stele. The piliferous layer was formed by the dermatogen and is homologous with the epidermis of the stem, but differs from it in that, whereas the epidermis is concerned with the restriction of water-loss, the piliferous layer is concerned with the absorption of water. The root-hair is a single living cell with a cellulose wall, inside of which is a layer of cytoplasm containing the nucleus and enclosing a vacuole with a colourless cell-sap.

The cortex consists of rounded parenchymatous cells containing small starch grains and includes numerous small intercellular spaces which facilitate the respiration of the tissue. The endo-

dermis is more obvious than that of the stem. It is composed of rectangular cells fitting closely together and whose radial walls are suberised.

The stele is characterised by the arrangement of its vascular tissues, the xylem and phloem groups being situated on distinct radii in contrast to their disposition in the collateral bundles of the stem. There are usually four rays of xylem alternating with a similar number of phloem groups. Each xylem group consists of an outer, *exarch* protoxylem and an inner metaxylem, the centre of the stele being occupied by a large metaxylem vessel, instead of the medulla characteristic of the stem. The xylem and phloem are composed of the usual Angiosperm elements and in this region of the root no cambium exists, the xylem and phloem being separated by parenchyma in which the cambium arises later. The outermost part of the stele is the pericycle consisting of a single layer of small cells immediately within the endodermis.

In that part of the root where the root-hairs are dying, and which is slightly older than the part so far described, two additional features will be seen. The walls of the cortical cells below the piliferous layer have become suberised, cutting off the outer cells from nourishment and causing their death. This suberised layer is the *exodermis*, which, owing to the impervious nature of its walls, functions in the same way as a cutinised epidermis. It serves to prevent the loss of water from the older parts of the root, which may be subjected to drying conditions especially during periods of drought. It is only the younger portions of the root which are concerned with the absorption of water, and once the suberised exodermis has been formed, absorption can no longer take place at that point. The other new feature of this region of the root is found in the stele, a series of strips of cambium having now appeared between the xylem and phloem groups. The cambium is formed by the division of parenchymatous cells to the inside of each group of phloem.

The mode of origin of the lateral branches of the root can be studied in the bare region immediately below the part which has branch roots at the surface. Each lateral root arises, some time before it becomes obvious at the exterior of the root, by the division of certain pericyclic cells, commonly opposite to the protoxylem. A new root-apex is formed within the endodermis, and this elongates to force its way through the cortex until it reaches the surface of the root. On its passage through the cortex the tissues of the lateral root are produced, being similar to those of the main root, so that on its arrival at the outside of the parent-root, the lateral root has a root-cap, and a central stele continuous with that of the root

which bears it. The origin of lateral roots from the stele is a characteristic of roots in all classes of vascular plants; the method is described as *endogenous*.

Other Dicotyledon roots differ little in structure from the buttercup root except in minor details. The number of xylem rays is not invariably four, but may be two (e.g. wallflower), three (e.g. elder), five (e.g. poplar) or even more, although a small number is usual. On this character a stele is described as *diarch*, *triarch*, *pentarch* and so on, the buttercup root stele being *tetrarch*. Another variation which may occur is the presence of a medulla in the centre of the stele. Many Dicotyledon roots agree with the buttercup in having no medulla, but others, such as broad bean, poplar and monkshood, have a well-defined parenchymatous medulla.

(e) **Monocotyledon Root.** So far as general structure is concerned, there is little difference in anatomy between the root of a Monocotyledon and that of a Dicotyledon. The root of the onion (Fig. 41, B), for example, has a large cortex and small central stele which is pentarch and possesses no pith. The more usual type of Monocotyledon root has a medullated stele and a higher number

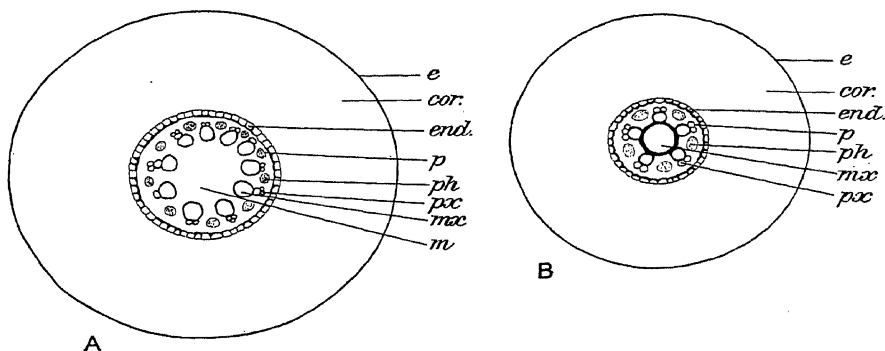


FIG. 41.—Monocotyledon Roots. Plan of tissues in transverse section.

A, Maize; B, Onion (*Allium*).

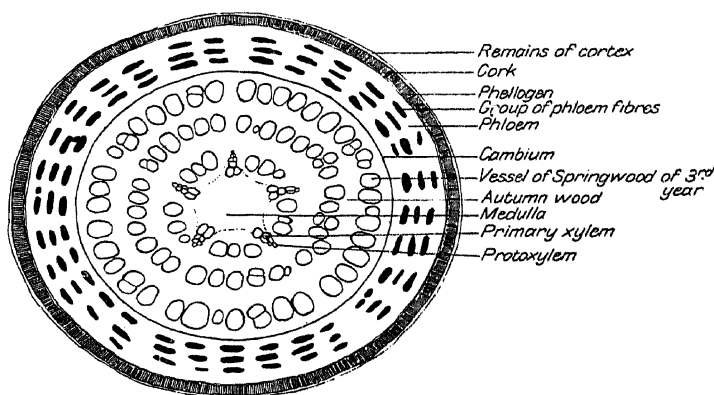
(cor. = cortex, e = exodermis, end. = endodermis, m = medulla, mx. = metaxylem, p = pericycle, ph. = phloem, px. = protoxylem.)

of xylem groups than is found in Dicotyledons. The maize root (Fig. 41, A) may be considered typical and shows a wide cortex and a small stele bounded by a thickened endodermis. The stele may have fifteen or more groups of xylem arranged radially at the periphery of a large parenchymatous medulla. Phloem groups alternate with the xylem, but no cambium occurs at any stage in the growth of the root. The *polyarch* stele and medulla are both

common features of Monocotyledon roots ; in some plants, including lily of the valley, the central medulla is lignified.

(f) **Woody Dicotyledon Root.** In the woody Dicotyledons, secondary growth in the stem is accompanied by the same process in the root.

The early stages of secondary growth in the root differ slightly from those in the stem. The cambial strips first form additional xylem in the bays of the primary xylem, which results in the cambium and phloem being pushed outwards towards the pericycle (Fig. 33, E). The cambial strips form arcs of a circle which becomes completed by the development of cambium in the parenchyma outside each protoxylem group. The general effect is to produce an arrangement in the root very similar to that in the stem of the



. 42.—Plan of tissues in transverse section of woody root of Poplar.

same age (Fig. 33, F). In subsequent years the behaviour of the cambium is identical with that of the stem, so that a compact woody cylinder is formed, on the outside of which is the cambial ring and a narrow zone of secondary phloem (Fig. 42). The cambium of the root also forms medullary rays, and in some roots, the primary rays are broader than the secondary rays, and are opposite to the protoxylem groups.

Although the cambium forms secondary xylem with broad and narrow vessels during the growing season, there is never such an obvious occurrence of annual-rings as in the woody stem.

Whilst the vascular system of the root is undergoing enlargement the exodermis becomes replaced by a corky bark. The phellogen of the root arises in the pericycle, so that the whole of the cortex is deprived of nourishment as the cork-layers are formed. This

leads to the death of the cortex, which during the early stages of cork-formation, forms the outer part of the bark, although later on it peels off or decays (Fig. 37, c). Lenticels may be formed in the bark of the root in a manner similar to that in the stem by the special behaviour of certain regions of the phellogen.

The Leaf

Leaves always arise as lateral outgrowths of the stem, mainly owing to the enlargement of localised parts of the periblem. Each leaf is formed by the division of periblem cells which first form a small protuberance (Fig. 27). This swelling pushes out the dermatogen (which will later form the epidermis of the leaf continuous with that of the stem), and continues to enlarge until it has formed an expanded leaf. The mode of origin of the leaf, from the outer tissues of the stem, is described as *exogenous*. The younger leaves near the apex of the stem may curve over it, so forming a bud (Fig. 27), the expansion to form a typical foliage leaf taking place when the leaf has become more remote from the apex.

The mature foliage leaf is characteristically a thin, green broad organ. Anatomically, foliage leaves are of two main types, both of which are *bifacial* as they have two distinct surfaces.

In most Dicotyledons, and a few Monocotyledons the leaf is *dorsiventral*, possessing an upper, or *ventral* surface, which differs from the lower, or *dorsal* surface, both in appearance and anatomically.

In many Monocotyledons and rarely amongst Dicotyledons, the leaf is *isobilateral*, having two surfaces which are more or less similar in appearance and structure.

(g) **Dorsiventral Leaf** (Fig. 43, A). The evergreen leaf of the cherry laurel (*Prunus laurocerasus*) is a good example of a dorsiventral leaf. It consists of a broad lamina, narrowing to a thin petiole which broadens slightly at the base where it is attached to the stem. The lamina presents a dark-green glossy upper (ventral) surface and a light-green lower (dorsal) surface from which the larger veins project slightly. The lamina is bounded on the outside by a continuous epidermis, which for convenience may be considered as being composed of ventral and dorsal parts. The epidermis is composed of a single layer of tabular colourless cells fitting closely together.

The ventral epidermis (Fig. 44, A) forms a complete layer with no spaces between the cells whose outer walls are thickly cutinised, so preventing water-loss. The dorsal epidermis (Fig. 44, B) consists of cells like those of the upper epidermis, but not so heavily cutinised. In this tissue, however, stomata occur, being formed of pairs of

curved *guard-cells*, like those of the herbaceous stem. The guard-cells contain chloroplasts and have their walls thickened in such a way that, on the volume of their vacuoles increasing, curvature takes place and widens the aperture between them (Fig. 44, c). Between the two surfaces is a parenchymatous *mesophyll*, in which the veins are situated. Beneath the upper epidermis the mesophyll consists of two layers of cylindrical cells, the *palisade tissue*, below

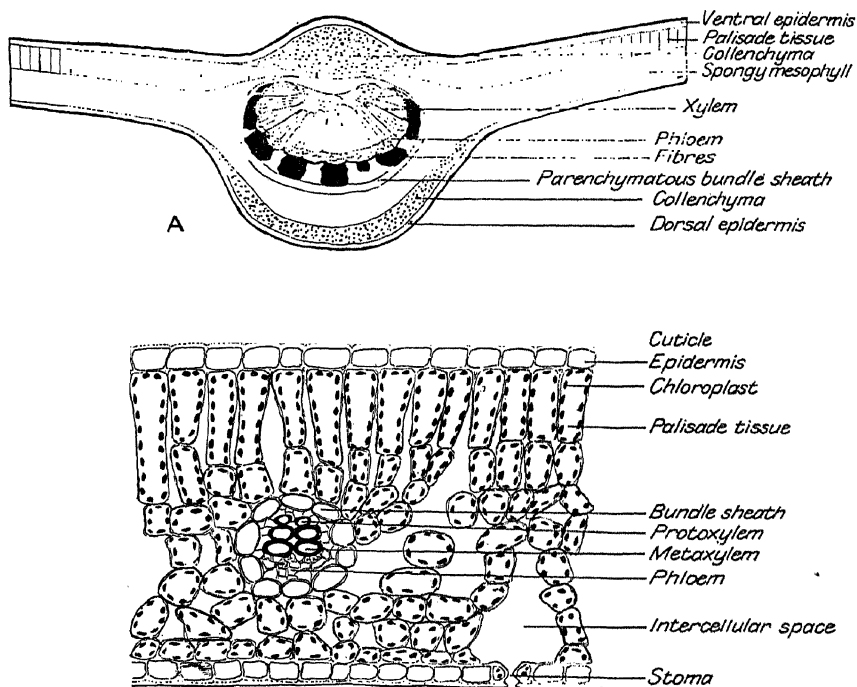


FIG. 43.—Cherry Laurel Leaf.

A, plan of tissues in transverse section through mid-rib region of lamina; B, detail of tissues.

which is the *spongy mesophyll*, reaching to the lower epidermis. The palisade cells have thin cellulose walls, and in their cytoplasm are many small discoid chloroplasts. Between the cells are narrow intercellular spaces which are best seen in sections parallel to the epidermis. The spongy mesophyll consists of rounded cells containing chloroplasts which are less numerous per cell than in the palisade tissue. Abundant intercellular spaces occur in this tissue, and these communicate with the atmosphere by way of the stomata.

The mesophyll is the chief photosynthetic tissue of the plant. The nature and arrangement of the palisade cells, whose long axes are at right angles to the leaf-surface, enables the leaf to absorb the maximum amount of light, and the intercellular spaces, especially of the spongy tissue, permit of the rapid gaseous exchanges required in the process.

The veins lie in the mesophyll below the palisade tissue. They provide mechanical support for the lamina and form the conducting system which is continuous with that of the stem. There is a main central vein, or *mid-rib*, continued from the petiole. It consists of a vascular bundle associated with parenchymatous and mechanical tissue (Fig. 43, A). The xylem of the bundle is directed towards the upper surface of the leaf, and below it lies the phloem.

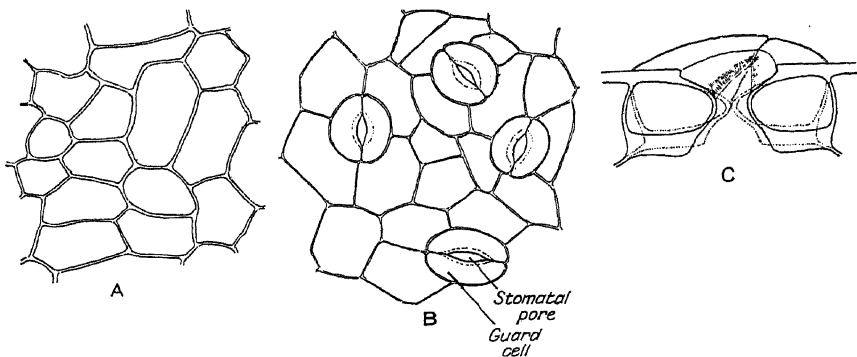


FIG. 44.—Epidermis of Cherry Laurel Leaf.

A, surface view of ventral epidermis; B, ditto, dorsal epidermis; C, stoma in section view (continuous line represents condition with guard-cells turgid, and dotted line with guard-cells flaccid).

In the mature leaf no cambium is present. Beneath the phloem are several groups of non-lignified fibres, and additional mechanical tissue is provided by thickened ridges of collenchyma running lengthwise above and below the bundle. Above the mid-rib the palisade tissue is modified and sometimes interrupted, whilst below, the ordinary mesophyll is replaced by colourless parenchyma.

The xylem of the mid-rib is composed of vessels and parenchyma, and the phloem of sieve-tubes, companion-cells and parenchyma, the whole bundle being enclosed by a bundle-sheath of parenchyma.

The lateral veins are not so complex, but their bundles are very similar to that of the mid-rib. As the veins branch repeatedly they become simpler in structure until they form *bundle-ends* which terminate amongst the mesophyll cells. The bundle-end

consists of a few spirally-thickened tracheids surrounded by a parenchymatous sheath, no typical phloem being present. It is the bundle-ends which distribute watery solutions to the mesophyll cells and collect up the food manufactured in them during photosynthesis.

All dorsiventral leaves are not exactly like the cherry laurel leaf but may show slight differences in both epidermis and mesophyll. The epidermal cells may be prolonged to form hairs of different types, some being *glandular* and having cells which form ethereal substances, others being non-glandular or *covering* hairs. Stomata may be present in both surfaces as in the broad bean and deadly

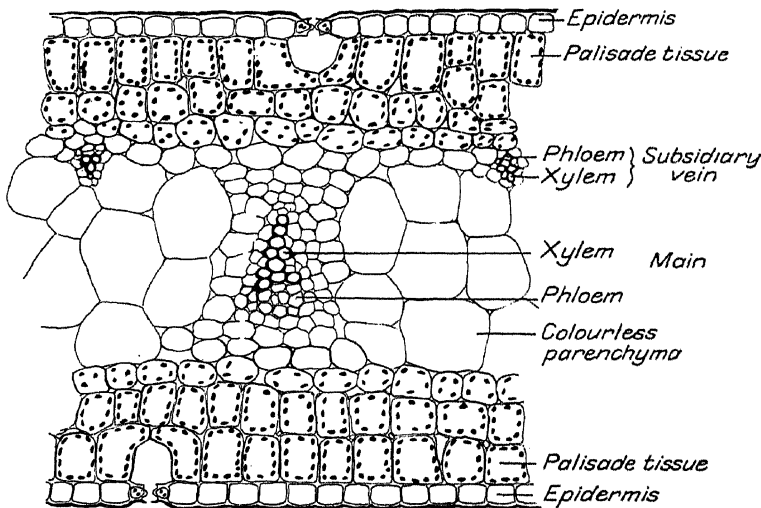


FIG. 45.—Part of transverse section of *Narcissus* leaf.

nightshade, but in this case the number per unit area is greater in the lower surface. The frequency of stomata in leaves varies from about one hundred to nearly two thousand per square millimetre, the average being about two hundred as in the cherry laurel. The palisade tissue of most dorsiventral leaves is but a single layer as in broad bean, henbane, and foxglove leaves.

In the leaves of stems possessing bicollateral vascular bundles, the main veins have also bicollateral bundles, an additional phloem being situated above the xylem.

(h) **Isobilateral Leaf.** The most typical examples of this type are found in the linear erect leaves of many Monocotyledons.

The leaf of *Narcissus* (Fig. 45) is an elongated organ arising from

the compressed stem of a bulb. It is not differentiated into lamina and petiole, the ribbon-like aerial portion widening below ground to form a fleshy bulb-scale. Owing to its erect habit, both surfaces of the leaf are similar, but actually there is an inner (ventral) surface and an outer (dorsal) surface decided by the origin of the leaf on the stem. The two surfaces have a similar appearance in microscopic examination, each being formed of elongated epidermal cells. Stomata occur equally in both surfaces and are generally similar to those of the cherry laurel. The mesophyll consists of one or two rows of short palisade cells beneath each epidermis, and a central part formed of rounded parenchymatous cells with thin walls. Veins run longitudinally in the central mesophyll, giving rise to the parallel venation so common amongst Monocotyledons. The larger veins have collateral vascular bundles in which the xylem, like that of the veins of the cherry laurel, faces the ventral surface. Between the larger veins are small veins which are closer to one epidermis than the other. These veins have their phloem facing the nearer epidermis, so that in all of them the xylem is directed inwards.

Some leaves have an internal structure intermediate between dorsiventral and isobilateral. In the senna leaflet a palisade tissue occurs next to each epidermis, but the upper palisade cells are deeper than the lower.

In the blue gum (*Eucalyptus globulus*) the first-formed leaves are sessile (without a petiole) and dorsiventral, whilst those formed later are petiolate and of somewhat similar structure to those of senna.

Many anatomical variations of the leaf occur in connection with the plant's environment, particularly in those plants of dry habitats where modifications are connected with the more effective prevention of water-loss. Such leaves may be of the type described as *centric*, and no longer are of the bifacial type. Centric leaves have a central stele surrounded by mesophyll bounded by a thickened epidermis, as, for example, the pine leaf (Fig. 79) which has a needle-like appearance, and offers little surface to the atmosphere.

CHAPTER VII

PLANT NUTRITION. ESSENTIAL ELEMENTS. ABSORPTION OF WATER AND MINERAL NUTRIENTS. TRANSPIRATION. HYDROPHYTES AND XEROPHYTES

During the growth of the plant it is constantly forming new materials, including protoplasm, cell-wall substances and foods, which are built up by the activity of the existing living cells.

In order to carry out the synthesis or building up of organic matter, the cells must be provided with certain inorganic raw materials. The typical green plant derives its raw materials partly from the soil and partly from the atmosphere. Although the chemical analysis of a plant shows it to contain a large number of chemical elements, these are not all of necessity essential for its normal growth.

Essential Elements in Plant Nutrition

It has been shown experimentally that, when a green plant is grown in an atmosphere containing carbon dioxide, it will thrive only when provided with a weak solution containing the following chemical elements: hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, iron and chlorine.

To ascertain the need for these elements young plants are grown in culture solutions. A *complete culture solution* contains the elements mentioned, in such a form and concentration as to resemble, approximately, the soil solution. The following is a suitable formula:

Calcium Nitrate .	0.8 gramme
Potassium Nitrate .	0.2 gramme
Potassium Phosphate	0.2 gramme
Magnesium Sulphate	0.2 gramme
Ferric Chloride .	a trace
Water . . .	1 litre.

Some young plants, such as small seedlings with little food reserves, are grown in this solution, whilst others are provided with *deficient solutions*, from which a particular element has been omitted. From a large number of experiments, carried out on a

variety of green plants, it has been found that the plant will only grow normally when provided with the complete solution, the absence of any element causing sickness and ultimate death.

The elements of the complete culture solution, together with carbon provided by atmospheric carbon dioxide, are called the *essential elements*. Although it is generally true that green plants require no more than the elements detailed in order to grow healthily, much evidence has accumulated in recent years of the need of certain plants for minute traces of additional elements. The broad bean requires almost infinitesimal amounts of boron, without which its root-tips blacken and die, and other plants require traces of zinc and manganese. Plants grown in deficient culture solutions develop symptoms according to the particular element that is absent. The absence of iron produces very striking results, and organs, such as leaves, which are normally green, fail to form chlorophyll and present a sickly yellow appearance described as *chlorosis*. Chlorosis can soon be abolished in this case by the addition of a small trace of iron to the solution. Chlorosis may occur in the absence of magnesium (which is a constituent of chlorophyll), potassium and calcium. The presence of too much calcium may also cause chlorosis, but this is probably because it prevents the entry of iron into the plant. Nitrogen is a constituent of proteins, and therefore of protoplasm, and in its absence the plant remains stunted and finally dies. Sulphur and phosphorus are also found in certain proteins, phosphorus occurring particularly in the nucleus, and in their absence poor growth and retarded cell-formation result. Phosphorus appears to play a part in the activity of some enzymes (p. 109) which cannot carry out their usual reactions in its absence. For example, with a deficiency of phosphorus the digestion of insoluble carbohydrate reserves may be prevented. Potassium may be involved in photosynthesis, for in its absence there is a lack of carbohydrate reserves in the plant.

With the exception of carbon, the essential elements are obtained from the soil under natural conditions. The soil contains a dilute watery solution which is a mixture of the sulphates, chlorides, nitrates, phosphates and bicarbonates of calcium, potassium, sodium, magnesium and iron. Some of the mineral matter of the soil may not be readily soluble in water, but its solution is assisted by such acids as carbonic, lactic, acetic and butyric, which are formed by the respiratory and fermentative activities of soil organisms.

Absorption of Water

Water forms a large part of all plant tissues, forming some 90 per cent of fresh herbaceous tissue and about 50 per cent of woody

tissues. It occurs as part of the living protoplasm, which consists of about 80 per cent water, in the cell-sap, and in the lumina of vessels and tracheids. Water is essential to growth for a number of reasons. It is necessary for the formation of active protoplasm, it provides the medium for the transport of organic and inorganic material in the plant, and is a raw material in the process of photosynthesis. Land plants obtain water from the soil by means of their root systems which take up that present in a large volume of soil, because of their extensive branching. Available water is present in the soil spaces and as a thin film around the soil particles, and the elongated root-hairs provide an efficient means of getting into intimate contact with this water.

The method by which water is absorbed depends, to some extent, on the nature of the plant cell. Young cells with thin walls and solid protoplasts *imbibe* water because of the colloidal nature of their protoplasts which act in a very similar manner to a piece of gelatine placed in contact with water. This method is used to a small extent by roots, where it occurs at the tips, and by the cells of seeds prior to their germination. In the case of mature cells which possess vacuoles water is absorbed by a method which involves *osmosis*. Osmosis is a physical phenomenon which takes place when two solutions of different concentration are separated by a type of membrane described as *semipermeable*, which permits the ready passage of the solvent (water) but prevents the passage of the dissolved solutes. The process may be demonstrated in the following manner. A thistle funnel is filled with a strong solution of sugar, and its mouth is then closed with a piece of pig's bladder, or cellophane, which is not readily permeable to sugar. The funnel is then placed in distilled water, when, after several hours, the volume of the water in the funnel will be found to have increased, indicated by a rise of the solution in the tube connected to the funnel (Fig. 46). This diffusion of water into the stronger solution through the membrane depends on the difference between the concentration of the solutions on the two sides of the membrane. If the funnel had been filled with water, and then placed in water, no difference in volume would have been brought about. The entry of water by osmosis, into a stronger from a weaker solution, sets up a pressure called *osmotic pressure*, which could be measured, in the experiment described, by attaching a mercury manometer to the tube of the funnel. Theoretically, osmosis takes place through a semipermeable membrane until the concentrations on both sides of the membrane are equal. When this condition is reached there is no osmotic pressure, for this varies directly with the difference in concentration of the separated solutions.

In the mature plant cell, the wall can be regarded as readily permeable to all solutions, but the lining layer of cytoplasm behaves as an osmotic membrane, although, as will be seen later, it is not perfectly semipermeable. When the cell is bathed with a liquid of lower concentration than that of the cell-sap within, water passes osmotically into the vacuole, setting up an osmotic pressure inside the cell.

Osmosis, however, is not the only factor concerned in the absorption of water by plant cells. If a cell-wall were not present the

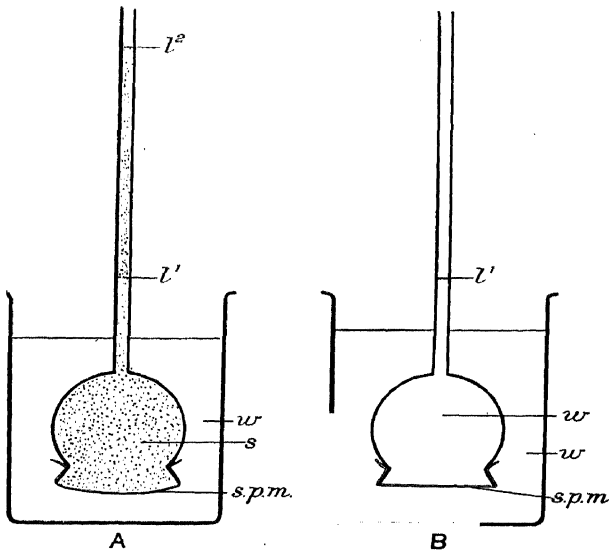


FIG. 46.—Experiment to demonstrate Osmosis. Description in text.

(l^1 = original level, l^2 = second level, s = sugar solution, $s.p.m.$ = semipermeable membrane, w = water.)

entry of water into the vacuole by osmosis would continue until the solutions on the two sides of the cytoplasm were in osmotic equilibrium. As the strength of the cell-sap is frequently much higher than that of the watery solution outside the cell, the osmotic pressure developed might cause the cytoplasm to burst and result in the death of the cell. The cellulose cell-wall is slightly extensible, but restricts the enlargement of the cell beyond a certain point. As the volume of the vacuole increases, so setting up an osmotic pressure against the cytoplasm, the cytoplasm is forced against the wall, which at first distends. The wall undergoing distension resists the force from within, to some extent, and sets

up a counter-pressure against it, known as the *wall-pressure*. When the wall reaches the limit of its extensibility its counter-pressure is maximal, being equal and opposite to the osmotic pressure tending to distend it. A cell in this condition is described as *turgid*, and has no further power of absorption. When a cell is turgid its cell-sap may still be denser than the solution outside, and theoretically capable of producing osmosis. It is for this reason that a plant cell is said to absorb water by a *suction force* or *pressure*, which, at any time, may be represented by the difference between the osmotic pressure (due to the difference in strength of the solution within and without the cytoplasm) and the wall-pressure (dependent on the state of the cell-wall). The suction pressure is usually stated thus :

where S is the suction force, P the osmotic pressure and T the wall-pressure.

In a fully turgid cell, the suction pressure is nil, whereas in a limp, or *flaccid*, cell, in which the cytoplasm is exerting no pressure against the wall, the suction pressure is equal to the osmotic pressure. As a flaccid cell absorbs water, wall pressure will soon be produced, and this increases to a maximum as the pressure of the cytoplasm against it increases to a maximum. Thus, as a cell passes from flaccidity to turgidity, the suction pressure decreases from its maximum value to nil. The absorption of water by the mature living cells of all parts of a plant is by the method described.

In the root of the land plant, the root-hairs are in contact with the weak soil solution. The cell-sap of the hair is stronger than the soil solution so that water enters the vacuole. The water absorbed by the root-hairs is required by all parts of the plant, and must, therefore, be transferred to the stele. It is usually assumed that, from the piliferous layer, water passes from cell to cell inwards through the cortex because of an increasing suction pressure gradient. As a root-hair absorbs water from the soil, its sap becomes more dilute than that of the cortical cell adjacent which, therefore, takes up water from the hair. From the outer cortical cell water will pass to the next cell within, and this process is repeated from cell to cell through the cortex as far as the endodermis (Fig. 47).

The mechanism of the entry of water from the cortex into the stele is unknown. Theories put forward include the idea of the endodermis acting as an osmotic membrane through which water diffuses from a supposedly weak cortical sap into a dense stelar sap, but the facts required by the theory are not yet established.

It is true that water is passed into the vessels and tracheids of the xylem with considerable pressure. This may be demonstrated by taking an actively absorbing plant, cutting off its shoot just above soil level and replacing it with a tube containing water attached to a mercury manometer. After a time a pressure exerted by the fluid exuding from the cut stump of the stem is indicated by the manometer; and this pressure, under favourable conditions, may reach a value of over one atmosphere. This pressure is called *exudation-* or *root-pressure*, which must be due to living cells, as it ceases when the root system is killed.

The rise of water in the xylem is easily demonstrated by placing the roots of a young leafy plant in a weak solution of eosin for a few days. If sections of the stem are then taken above the level of the solution in which the plant was standing, the vessels and tracheids will be found to be stained with eosin. Further proof

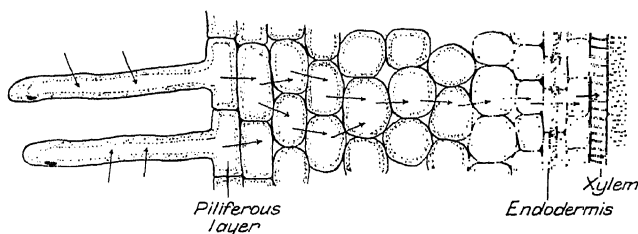


FIG. 47.—Longitudinal section of part of a root, to show passage of water from the soil to the xylem (denoted by arrows).

may be obtained by taking a woody twig bearing leaves, removing from it a ring of tissue, half an inch wide, to the depth of the xylem, and placing its end in eosin. After a time the eosin will be found to have risen in the stem above the level of the removed ring, and so could only have passed in the intact xylem. If the vessels and tracheids of the lower end of the stem are blocked with wax, and the experiment repeated, no rise of the solution will take place.

Absorption of Mineral Nutrients

So far, the entry of water and its movement within the plant have been considered. The entry of soil minerals into the plant and their subsequent movement within it are quite independent of the osmotic passage of water. There is no such thing as an osmosis of solutions, although solutions control the osmotic movement of water.

The cytoplasmic membrane of the cell is not a true semiper-

meable membrane, but can be described as a *differentially-permeable* membrane allowing certain solutes to pass more readily than others. That the cytoplasm is permeable to substances other than water may be demonstrated by mounting cells in a 5 per cent solution of glycerine, which is stronger than the cell-sap. In a short time water passes by osmosis from the vacuole outwards, causing the cytoplasm to contract from the cell-wall and producing a condition called *plasmolysis* (Fig. 48). After a further lapse of time, the cytoplasm will be found to have recovered its original condition, owing to the diffusion of glycerine into the vacuole, which results in the raising of the sap to a concentration equal to that outside and the establishment of turgidity.

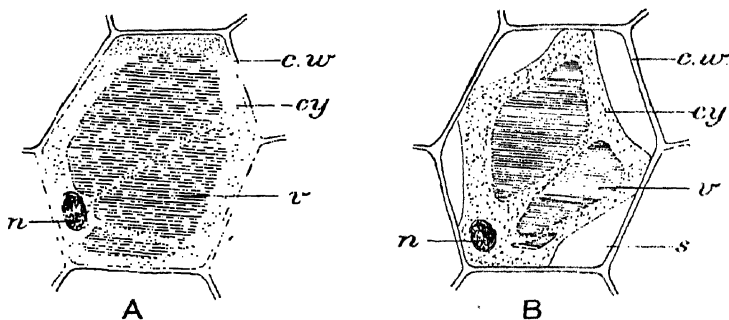


FIG. 48.—Plasmolysis.

A, normal condition of cell; B, condition when plasmolysed.

(c.w. = cell-wall, cy. = cytoplasm, n = nucleus, s = space occupied by plasmolysing fluid, v = vacuole containing cell-sap.)

The materials present in the soil solution are present in very dilute concentration, so that they normally occur in an ionic and not a molecular condition. These ions diffuse, as such, through the cytoplasm into the cell. The rate of entry of the ions of dissolved substances is governed by the permeability of the cytoplasm to them and by the concentration of free ions inside and outside the cell. The movement of ions is from a higher to a lower concentration, so that if an ion contains essential elements it will enter into chemical combination with other substances in the cell and thus will continue to be absorbed. If, however, an ion is not essential it will remain free in the cell, and the accumulation occurring will soon prevent the entry of further ions of the same kind. It is only in this way that the plant may be considered to exhibit a selective absorption, having no direct control over the ions which shall be permitted to enter.

Owing to the ionic entry of substances into the cell, it may be

found that for a substance such as calcium chloride, the individual ions, entering independently, do so at different rates. The garden pea absorbs calcium ions about five times as fast as chlorine ions, but in the runner bean chlorine is absorbed at a slightly quicker rate than calcium. The passage of ions is also dependent on a balance being maintained inside and outside the cell. If a positively charged ion enters the cell, it must be replaced by a similarly charged ion passing out. Therefore, when plants are grown in culture solutions hydrogen ions or hydroxyl (OH) ions may pass from the plant into the solution and, in due course, cause a change in acidity or alkalinity of the solution.

In land plants, once the soil solutes have entered the root-hairs, there will be a similar ionic diffusion between the cells of the tissues. Like the absorbed water, some of the ions will be used in the growth of the cells they enter, but many will reach the water in the xylem, which will become a reservoir supplying the needs of cells in various parts of the plant.

Transpiration

One of the important features of land plants is the loss of water from their aerial organs. As a large part of the plant consists of water, and as it is in contact with a relatively dry atmosphere, water will be lost by evaporation. The process of water-loss from the shoot is called *transpiration*, and it may be very great under some conditions. It has been calculated that a large sunflower plant loses about a pint of water a day during the summer, and that a large beech tree, having a tremendous leaf-surface, loses about 100 gallons a day.

Transpiration may be demonstrated by placing a leafy plant beneath a cool dry bell-jar for some hours when the water vapour given off will have condensed on the sides of the bell-jar. Another experimental method involves the use of cobalt chloride paper, which is blue when perfectly dry and assumes a pink colour when in contact with moisture. If pieces of dry cobalt chloride paper are placed on each side of a leaf, and protected from the atmosphere by dry glass plates, it will be seen, after a time, that the paper has become pink owing to the vapour given out in transpiration.

Transpiration takes place chiefly from the broad surface of foliage leaves, although any young organ may lose some water. It can be shown that in ordinary plants the greater part of transpired water is lost from the stomata, for if the stomatal surface of a dorsiventral leaf is greased to block the stomata, the leaf loses less water (shown by loss of weight) than a control leaf with its stomata free.

Although *stomatal transpiration* is responsible for most of the water-loss, some water may be lost directly through the epidermal walls. Except in the case of young leaves, such *cuticular transpiration* is small in British plants, but may represent about 50 per cent of the total in certain tropical plants.

The main loss of water is from the mesophyll of the leaf, water passing from its cells to the intercellular spaces, and thence through the stomata to the atmosphere.

The rate of transpiration is not uniform but varies with those atmospheric conditions which influence evaporation. Thus, transpiration is greater on a dry day than on a wet day, when the air is saturated. It is generally greater on a sunny day, when there is increased radiation than on a dull day, and greater in wind than in still air, as on a calm day a saturated layer of air lies close to the leaf-surface, but this is moved quickly by wind.

Other conditions remaining the same, transpiration is less in the dark than in the light. The reason for this is associated with the behaviour of the guard-cells of the stomata. Guard-cells, as a rule, alter their turgidity quickly under various conditions. Owing to their shape and the disposition of the thickening of their walls, when guard-cells are turgid they curve and deepen, so causing the widening of the pore (Fig. 44, c). On becoming flaccid the cells resume their original position and tend to close the pore. It was formerly thought that this behaviour of the guard-cells had an important effect on transpiration, and that when a plant was subjected to conditions tending to accelerate transpiration, an early result was a loss of turgidity by the guard-cells with a closing of the stomatal aperture and the prevention of further water-loss. In recent years it has been shown that the guard-cells do not behave in this way, and that when the shoot has lost so much water that it *wilts*, or droops, the stomata may be widely open. Almost as much water-vapour escapes through a narrow stoma as from a fully open one, and not unless the pore is completely shut can stomatal transpiration be prevented.

The turgidity of the guard-cells is controlled by the photosynthetic process rather than by transpiration, the reasons for which will be considered later.

The rate of transpiration may be measured in a number of ways. In the case of an entire plant, the transpiration over a certain period may be ascertained by enclosing the root system in a pot from which no water can be lost, leaving only the shoot exposed. The weight of the plant is taken at the beginning and at the end of a period, and the loss is taken to indicate that due to the evolution of water-vapour. If the plant is exposed to different external

conditions, the loss of weight over a certain time will give an indication of the effect of the conditions on transpiration.

The transpiration rate of small shoots can be measured by an apparatus called a *potometer* (Fig. 49). The potometer consists of a tube into which the cut end of a shoot is placed and to which is attached a horizontal capillary tube, the tubes being filled with water. A potometer strictly measures the rate of absorption by the shoot, but this is assumed to balance exactly the water lost during transpiration, which, for demonstration purposes, is approximately true. As water is absorbed by the shoot, the end of the

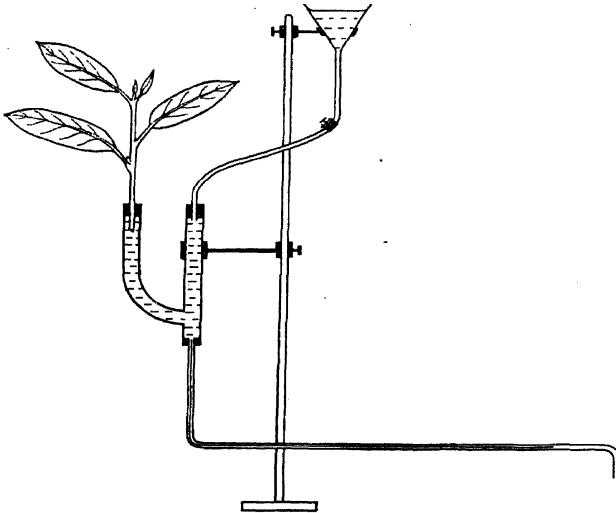


FIG. 49.-Potometer, for measuring the rate of transpiration of a leafy shoot (description in text).

water column in the capillary tube is drawn along, and the rate at which it travels gives a measure of the rate of transpiration. Many potometers include a water reservoir which enables the capillary tube to be easily refilled after each reading.

The continuous loss of water from the aerial system of a plant must be made good by absorption from the soil, if the plant is to be in no danger.

In land plants with aerial stems there is a continuous current of water passing in the xylem from the roots, through the stem and the veins of the leaves. The existence of this *transpiration current* has already been indicated in the experiments on the rise of coloured fluids in the stem.

In tall trees, the water entering the roots has to be raised to heights of a hundred feet or more, and there has been a certain amount of conjecture as to the forces which effect this rise of water.

Whilst root-pressure may play a part in small plants, it is quite insufficient to raise water to great heights, and theories depending on atmospheric pressure are untenable for the same reason.

A theory which is largely supported at the present time is the *Cohesion Theory*, first propounded by Dixon and Joly. This considers that, because of its great cohesive power, the water in the vessels and tracheids is similar to a solid rod or wire, which needs only to be pushed or pulled at the end for movement to be brought about. As the apices of the root and shoot elongate they add new vascular tissue to the ends of the water column. The forces producing movement include the propelling root-pressure below, but the most important is the suction applied to the top of the water column by the transpiring leaves. As water is lost from the mesophyll cells adjoining the intercellular spaces, their suction pressure increases. This enables them to take water from deeper-seated mesophyll cells which, in their turn, obtain it from the bundle-ends, to which a suction is applied.

Experiments have shown that a leafy shoot will raise a column of mercury so long as its leaves are living and transpiring, but when they are removed, or killed, the column is not maintained.

It will be appreciated from what has been said that the process of transpiration plays a part in the maintenance of a flow of water through the plant, but apart from this it seems certain that transpiration has no direct rôle. It would appear that the process is largely incidental, for as the plant contains so much water, and is exposed to a relatively dry atmosphere, it would lose water on physical grounds. An incidental effect of transpiration may be to prevent the overheating of the plant, for, of the radiant energy falling on a leaf, about 70 per cent is converted to latent heat of evaporation of water.

How far a plant is able to control its transpiration is problematic, but, if it does so at all, it is not by stomatal changes but owing to the colloidal nature of its tissues. Numerous experiments demonstrate the fact that, when a shoot loses water, a point is reached when the tissues retain water against great drying influences, even when the stomata are open. This control of transpiration is associated both with the colloidal protoplasts of the mesophyll cells, and their drier cellulose walls, which are much less permeable to water vapour than when they are wet.

Mesophytes, Hydrophytes and Xerophytes

The above considerations of the water relations of the plant have referred mainly to plants growing under average conditions of water supply, such as are encountered in the majority of habitats of temperate regions. Such plants are called *mesophytes*.

Plants exist which differ widely from mesophytes in their water relations and are either *hydrophytes* or *xerophytes*.

Hydrophytes (Fig. 50) are plants inhabiting water, being either completely submerged, like *Elodea*, or having submerged and aerial organs, as in frogbit and water-lily. The submerged organs exhibit structures connected with their environment, including absence of cuticle and stomata from leaves and stems, poorly developed xylem, abundant intercellular air-spaces, and absence of absorbent roots.

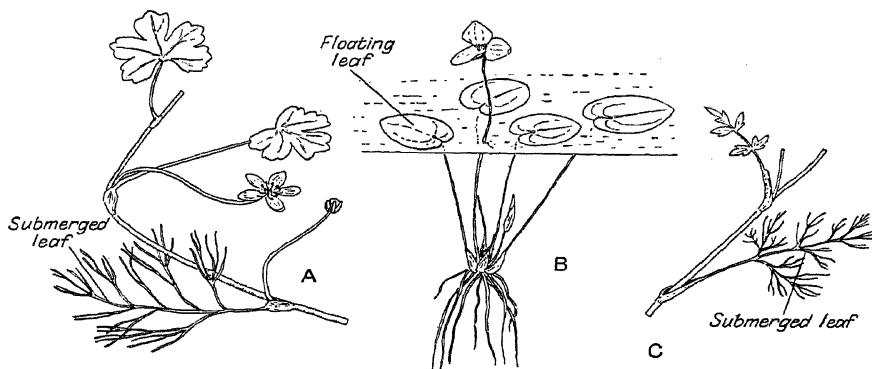


FIG. 50.—Hydrophytes.

A, *Ranunculus aquatilis* (Water Crowfoot); B, *Hydrocharis morsus Ranae* (Frogbit); C, *Apium inundatum* (all $\times \frac{1}{2}$).

Submerged aquatics obtain their nutrients, mineral and gaseous, in solution from the surrounding water, being able to absorb them at all points because of the absence of cuticle. On account of this ready entry of materials, there is little necessity for an elaborate conducting system and, commonly, the xylem is reduced to parenchyma, or a few unligified vessels (Fig. 51). The gases needed for respiration (oxygen) and photosynthesis (carbon dioxide) are obtained from the water, so that stomata are not required for gaseous diffusion into and out of the plant. As the solubility of oxygen in water is low, the internal tissues might experience some difficulty in respiring, were it not for the great development of air spaces (Fig. 51) which provide an internal system in which oxygen, formed in photosynthesis, can be retained and circulated to poorly aerated parts.

Xerophytes are plants growing under conditions of extreme drought, in such habitats as deserts and other dry places. As most xerophytes have modified shoot systems, it is usually thought that the plants can live under dry conditions because of their specialised structure, which is assumed to cut down transpiration. Whilst it is true that the modifications found in plants of dry places involve reduced leaf-surface, it is now doubted that this serves to prevent transpiration. It appears that many xerophytes transpire freely, but whereas extreme water-loss would produce desiccation and death in mesophytes, the protoplasm of xerophytes can undergo partial desiccation but recover and resume its activity. The characters generally associated with xerophytism include reduced leaf-surface (e.g. pine, Fig. 78, cypress), sunken stomata (e.g. pine) thick cuticle (e.g. pine, cherry laurel), and

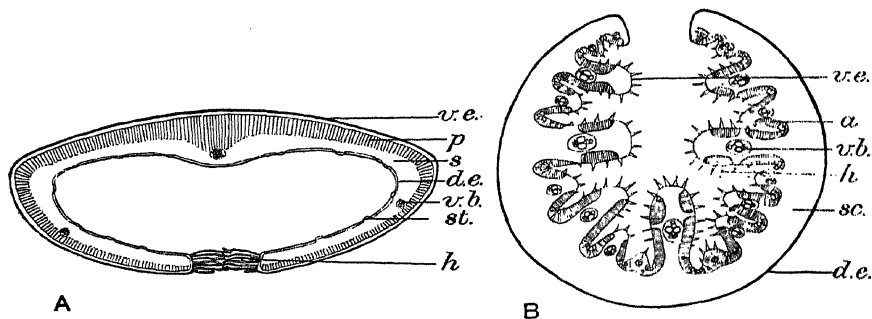


FIG. 53.—Xerophytic Leaves. Plan of tissues in transverse sections of A, Crowberry (*Empetrum*), B, Marram Grass (*Psalamma*, = *Ammophila*).

(a = assimilating tissue, d.e. = dorsal epidermis, h = hair, p = palisade tissue, s = spongy tissue, sc. = sclerenchyma, st. = stoma, v.b. = vascular bundle, v.e. = ventral epidermis.)

succulent. water-storing tissues (e.g. aloe, cacti). The reduction of leaf-surface may be brought about in several ways. In the gorse and cacti the leaves become spines, in the heather (Fig. 52) the narrow leaf has a rolled margin, in the crowberry (*Empetrum*, Fig. 53, A) the leaf is permanently rolled into a cylinder, enclosing the stomatal surface, and in the marram grass (*Psalamma*, Fig. 53, B) the linear leaf furls up under very dry conditions to enclose the stomatal surface.

It is now known that certain plants possessing one or more of the features associated with xerophytism are not true xerophytes, as they never actually suffer from a shortage of water and are not drought-resistant.

An example of a true xerophyte is the creosote bush (*Larrea*), a native of the Arizona Desert. It is a small shrub, with small

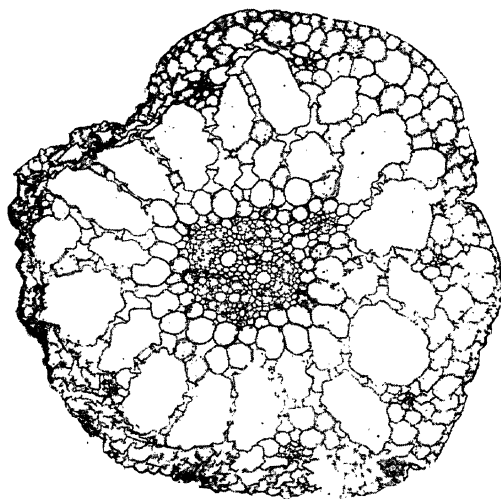


FIG. 51.—Photomicrograph of a transverse section of the stem of Frogbit, a hydrophyte.

Note the large air-spaces in the cortex, and the poorly-developed xylem in the central stele.



FIG. 52.—Photomicrograph of a transverse section of the leaf of heather (*Erica tetralix*).

The lower surface bears stomata, protected by hairs, and by the rolled margin of the leaf.

slightly-hairy leaves having a varnish-like surface. At the onset of the dry season the leaves lose water and wilt, and, if drought is prolonged, some of the leaves die and are shed. Within a few hours of the arrival of rain, the plant revives, its leaves recover and transpire as vigorously as those of a mesophyte. This indicates that xerophytism does not necessarily imply a restriction of transpiration. The important fact is that *Larrea*, and similar plants, possess protoplasm with the ability to remain alive despite some desiccation.

Xerophytes, such as the desert cacti, which possess fleshy stems are called *succulents*. They store large amounts of water in their tissues, which often contain mucilaginous materials having great powers of taking up water. When water is available, during the wetter periods, it is stored, and conserved carefully during the dry periods, owing to the nature of the storage tissues, assisted by a thickly cutinised epidermis with few stomata. The stomata are generally closed for a large part of the day, even in the light. Such succulents never experience an internal water-shortage, no matter what the external conditions may be, which is evidenced by the following experiment. A certain succulent, *Echinocactus*, was uprooted and stored in a laboratory under dry conditions. At the end of six years the plant had lost but 0.03 per cent of its original weight, and was alive and growing satisfactorily at the expense of the material originally present.

There are certain fleshy plants which superficially resemble the cacti, and were thought to be xerophytic. They are the *halophytes*, or salt-marsh plants, including the glasswort (*Salicornia*), found in muddy estuaries in various parts of Britain. It was assumed that halophytes experienced difficulty in absorbing the salt water, which saturated the soil in which they grew, and only absorbed diluted water (as after rainfall), and stored it for later use. It is now known that halophytes experience no such difficulty in absorption, nor do they conserve the water in their tissues but transpire as freely as mesophytic plants. If they were uprooted, as was *Echinocactus*, wilting would take place within a few hours, and there would be no recovery from it. Halophytes are not xerophytic, as their protoplasts cannot survive after drying.

The plants of bogs, heaths and moorlands are usually characterised by a reduced leaf-surface, explained as a control over excessive transpiration. Whilst it is true that reduced surface and protected stomata may delay the occurrence of wilting, it is found that, in relation to the amount of root available for absorption, bog and heath plants transpire considerably and do not normally suffer water-shortage.

The term *xeromorph* has been suggested for those plants which possess the characters of xerophytes yet have no power to withstand prolonged drought.

It might be mentioned, in conclusion, that most seed-plants are xerophytic in their seed stage, for, as a seed is ripening from the ovule stage, water is lost without the death of the protoplasm. After dispersal a seed takes up water, which revives the dormant protoplasm, and germination proceeds, but, in all but true xerophytes, the active protoplasm can now no longer undergo drying without death.

A true xerophyte is therefore a plant which has retained the seed type of protoplasm throughout its life.

CHAPTER VIII

PLANT NUTRITION. PHOTOSYNTHESIS. NITROGEN ASSIMILATION. INSECTIVOROUS PLANTS. HETEROTROPHIC PLANTS

The raw materials absorbed by green plants are utilised in the formation of organic material, much of which becomes food to be used for growth and other processes. Those processes which are concerned with both the building-up of food, and its ultimate utilisation, are collectively called *metabolism*.

The metabolic processes may be *anabolic*, which result in the formation of food, or *katabolic*, in which food is broken down to provide energy.

Photosynthesis

The most important anabolic process in green plants is *photosynthesis* or *carbon assimilation*.

Photosynthesis goes on in green tissues during their exposure to light, and results in the formation of simple foods, viz. sugars.

The greatest proportion of the solid matter of plants is carbon, which represents about 50 per cent of their dry weight. This carbon is derived entirely from the small proportion of carbon dioxide in the atmosphere.

In 1630 van Helmont grew a small willow shoot in a known weight of soil and watered it daily for a period of five years. During this time the plant increased in weight by over 100 pounds whilst the soil lost only 4 ounces. From this he concluded that the bulk of the plant was produced by the water.

In 1779 Priestley discovered oxygen ("dephlogisticated air") and found that green plants could form it from the air rendered impure by animal respiration, which is now known to contain carbon dioxide.

In 1798 Ingenhousz proved that, in the light, green plants absorbed carbon dioxide and evolved oxygen, and that the only source of the plant's carbon was the atmosphere.

It is easily proved that the green plant requires gaseous carbon dioxide, as when it is grown continuously in an atmosphere devoid of this gas it ultimately dies.

Photosynthesis consists in the combination of carbon dioxide and water in green cells to form sugars, and in many plants this is followed by the formation of starch. Starch-formation in green cells occurs in such common plants as sunflower, primrose and *Pelargonium*, which form suitable subjects for experiments on photosynthesis. Although starch-formation itself is not a direct proof of photosynthesis, when it occurs in green tissues, it is because of the previous occurrence of the process in those cells. Therefore, if the green tissues of a suitable plant are found to form starch under certain conditions, it is permissible to assume that those conditions are necessary for photosynthesis to go on.

The chief factors necessary for photosynthesis are :

1. Light.
2. Chlorophyll.
3. Carbon dioxide.
4. Water and certain salts.
5. A suitable temperature.

In experiments carried out to show the necessity of the factors in photosynthesis, employing the formation of starch, it is essential to commence with plants whose leaves contain no starch, and to conduct control experiments at the same time.

The destarching of the leaves of a plant, like *Pelargonium* (garden geranium), assumes the necessity of one of the essential factors in photosynthesis. If the plant is kept in a dark cupboard for 12 to 24 hours, and its leaves then tested for starch, none will be found to be present. To investigate the presence of starch in green leaves requires the following procedure. The detached leaf is killed by immersion in boiling water, transferred to alcohol and left until all the chlorophyll has been extracted, when the leaf has a white appearance. It is then softened in warm water and tested with iodine solution. If starch is present, the bleached leaf assumes a grey-black colour, but in the absence of starch a yellow-brown iodine stain results.

To demonstrate the necessity of light in photosynthesis, a destarched plant is placed in an ordinary atmosphere for several hours exposed to light and a similar plant is kept in a dark cupboard. At the end of the period leaves from both plants are tested for starch, which will be found to be present only in those of the plant which received light.

Under ordinary conditions, 'white' light is used in photosynthesis, and this is composed of waves of different lengths which can be separated to form the colours of the spectrum, viz. red, orange, yellow, green, blue, indigo and violet. That the different wavelengths of light are not of equal value in photosynthesis can be

demonstrated by a simple experiment. If a screen is made of strips of transparent gelatine of various colours (Fig. 54, B) and this is placed over the leaf of a destarched plant, which is then exposed to light for several hours, the amount of starch formed will depend on the type of light reaching the leaf-surface. Most starch would be found beneath the colourless part of the screen, but almost as much would be formed below the red strip, somewhat less below the blue, and negligible amounts in the case of other colours (Fig. 54, B). This proves that the red rays are most important in the process, and that blue rays are also utilised, but that other waves are of little use. The light rays provide the energy for photosynthesis, but only those actually absorbed by the chloroplasts are used. Of the light which falls on a leaf only about 4 per cent is used in photosynthesis.

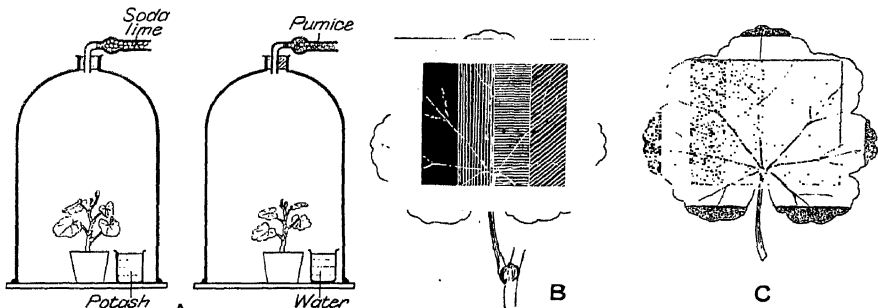


FIG. 54.—Experiments on Photosynthesis (description in text).

A, to show necessity of carbon dioxide; B, to ascertain the essential light rays: from left to right, colour screen consists of "white," red, blue and green strips; C, starch-print obtained from B.

That the chloroplasts of green cells are an important factor in photosynthesis can be demonstrated by using the *variegated* leaves of plants. Variegated leaves are those which have areas of green cells and yellow areas of cells containing no chloroplasts. If a variegated *Pelargonium* plant is destarched, and then exposed to light for a time, it will be found that the green parts of the leaf contain starch, but the yellow parts do not.

Of the pigments contained in the chloroplasts, only the chlorophylls are concerned with the absorption of light during photosynthesis. The chloroplast pigments can be extracted from leaves by solvents like alcohol and acetone. The solution obtained is green in transmitted light but shows a blood-red fluorescence in reflected light. By the use of other solvents, a separation of the crude extract from the chloroplasts can be made, and extracts containing chlorophyll *a* and chlorophyll *b* can be prepared. Impor-

tant features of solutions of the two chlorophylls are their absorption spectra,¹ which show deep black bands in the red part of the spectrum, and an almost complete absorption of the blue part. This indicates the wave-lengths absorbed by the chloroplasts, and the particular rays which are used in photosynthesis, and explains the reason for unequal starch formation in the leaf covered with a colour-screen.

Temperature also plays a part in photosynthesis, which, in common with other physiological processes, proceeds only at a suitable temperature. The range of temperature over which photosynthesis will proceed lies between a minimum in the neighbourhood of 0° C., and a maximum of about 45° C. Between this limit is an *optimum* temperature at which the process goes on at its maximum rate, other conditions remaining unchanged, the optimum lying between 28°–37° C. according to the plant. Some alpine and arctic plants carry out photosynthesis at temperatures as low as – 6° C., but it seems probable, in these cases, that the internal temperature of the plant is higher than that outside.

Carbon dioxide has already been mentioned as the raw material providing the carbon of photosynthesis. As, under ordinary conditions, the atmosphere contains only 0.03 per cent of the gas, it is clear that large volumes must be taken up by plants which accumulate abundant reserve foods. The need for carbon dioxide may be shown by using two destarched green plants, and growing one under conditions of carbon-dioxide deficiency, and one in normal air (Fig. 54, A). When leaves from both plants are tested for starch, after several hours' exposure to light, it is found in the leaf which had access to carbon dioxide, but not in the other.

In land plants carbon dioxide enters the mesophyll by way of the stomata, diffusing into the leaf at its own rate, independent of other gases in the atmosphere. The gas passes into solution in the moist walls of the mesophyll cells, especially the palisade cells, and diffuses into the cytoplasm to come in contact with the chloroplasts, where the actual process of photosynthesis occurs. In the case of submerged hydrophytes, carbon dioxide is present in solution in the surrounding water, which diffuses through the uncutinised epidermis of the plant into the green tissues below.

¹ *Note*.—When "white" light is examined with an instrument called a spectroscope, it is seen to be split up into the coloured bands of the spectrum. If a transparent red screen is inserted between white light and the spectroscope, only the red part of the spectrum can now be seen, the rest appearing black. This is because the red screen absorbs all but red rays, which it transmits. Therefore, in spectroscopic examination of a substance, if some part of the spectrum appears as a black line, the rays of this region have been absorbed by the substance.

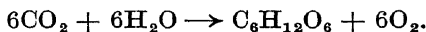
The full details of the photosynthetic process are not known, and there is little exact information as to what goes on inside the green cells. The simple facts known are, that carbon dioxide is absorbed, light energy is used, and sugars are formed.

During the process, oxygen is produced in the tissues as a by-product, which is given out from the plant. The evolution of oxygen may be demonstrated in submerged aquatic plants, such as *Elodea*. A few shoots are placed under a funnel in a beaker of water charged with carbon dioxide, a collecting-tube is placed over the funnel and the apparatus is exposed to light. After a time, the bubbles of gas given off by the plant accumulate in the tube, and when sufficient has been collected, the gas may be shown to be oxygen by testing with a glowing splint.

A more certain, but delicate, method of demonstrating the production of oxygen in photosynthesis was devised by Engelmann who used *aerotactic bacteria* as indicators. Aerotactic bacteria are microscopic organisms which swim from a region of low oxygen concentration to one of higher concentration. Engelmann mounted the filament of a Green Alga in a drop of cool boiled water containing *Bacterium termo*. The cover-glass was sealed to exclude external air, and the preparation placed in the dark until the bacteria had used the available oxygen and come to rest. The Alga was then exposed to light, and in a short time the bacteria had resumed their activity and had accumulated around the algal filament. This indicated the presence of oxygen in the vicinity of the Alga, and this had, presumably, been formed in photosynthesis. This method has been used to show which wave-lengths of light are most useful in photosynthesis. After removal from the dark of the preparation, a spectrum is projected along the length of the filament so that its various parts receive one type of light. In a short time it is found that most bacteria have accumulated in the region illuminated by red light, some occur in the blue region, but few elsewhere.

The evolution of oxygen and the removal of carbon dioxide from the atmosphere are important features of photosynthesis, apart from the food-forming aspect of the process. It is by this means that the composition of the atmosphere is maintained more or less at a constant. All living organisms are constantly removing oxygen during respiration, and emitting carbon dioxide into the atmosphere, and were it not for the purifying work of green plants, originally noted by Priestley, the atmosphere would soon be incapable of maintaining life.

Photosynthesis may be summarised by the following equation :

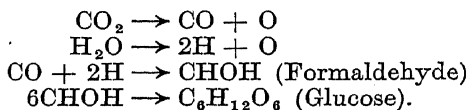


This indicates that the end products of the process are oxygen and a sugar, such as glucose, which is of the type called a *hexose*.

It is a common view that hexose sugars are the first foods built up in the process of photosynthesis, but it is almost certain that sugar is not the first substance formed by the combination of carbon-dioxide and water, but that it arises from intermediate substances.

The stages by which carbon dioxide and water give rise to sugars, and other carbohydrate materials, is largely a matter of conjecture.

Baeyer, in 1864, suggested that formaldehyde (CHOH) was an early product, because Butlerow, a few years before, had produced a sugar-like substance from dioxymethylene, which is a polymerised form of formaldehyde. The scheme suggested by Baeyer was as follows :



Since this theory was first propounded, many attempts have been made to demonstrate the occurrence, in the green leaf, of those reactions required to prove it. So far, little success has resulted from experiments on living tissues undertaken to detect the formation of formaldehyde, nor have experiments, in which green organs were provided with weak concentrations of formaldehyde, shown the increased carbohydrate formation which might be expected.

In 1921 and later, Baly produced a substance containing a proportion of hexose sugar, by treating formaldehyde with ultra-violet light. As he did not use living cells, and as ultra-violet light is unnecessary for plants to effect photosynthesis, Baly's results have little direct bearing on the behaviour of living plants. Despite the present difficulties in proving the formaldehyde hypothesis, the substance seems to be a likely stage in photosynthesis. It may be that the methods of detection of formaldehyde now available are unsuitable for living plant tissues, in which reactions may be very rapid, owing to the great surface energy provided by the colloidal protoplasm.

On the grounds of simplicity, hexose sugars appear to be the most likely carbohydrates to be formed first in photosynthesis. Nevertheless, the view is held by some investigators that a more elaborate sugar, cane sugar ($\text{C}_{12}\text{H}_{22}\text{O}_{11}$), is formed first. It is true that green leaves contain a number of sugars, and that these can be built up into more complex substances which, in their turn, can be broken down to simpler sugars again. Cane sugar, or sucrose, is peculiar to the plant kingdom, and is found to be a very suitable

substance for the formation of starch in plants. It is readily broken down to hexose sugars, both in the living cell, and by acids, and it is usually thought that, when it occurs in cells, it has been formed previously from hexoses.

After sugar has been produced in the green cells, other processes occur in most plants, but in several Monocotyledons, including the onion and the snowdrop, sugar remains unaltered, and may be carried to organs for storage. In those plants which form starch in their leaves, the sugar of photosynthesis is transformed to minute insoluble starch grains, which accumulate in the chloroplasts during the process.

The formation of starch, subsequent to photosynthesis, depends upon the concentration of sugar tolerated by the particular cell. In starch-forming plants, when the concentration of sugar reaches from 0.2 to 0.5 per cent (according to the plant), further sugar formed is built up into starch. In sugar-accumulating plants, the cells tolerate high concentrations of sugar (up to 30 per cent), and under natural conditions this is not exceeded, and no starch is formed.

Starch-formation can be shown experimentally to be influenced by the previous synthesis of sugar. Detached leaves of destarched plants can be induced to form starch in the dark, if they are kept for some days with their petioles immersed in a suitable solution of either glucose or cane sugar. The fact is indicated under natural conditions by the presence of starch in underground organs like tubers, corms, rhizomes and roots. Such organs could not have carried out photosynthesis owing to the absence of light, but have built up large grains of storage starch, from sugars that were passed down, in the phloem, from the aerial shoot.

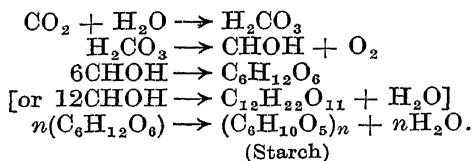
The starch present in the chloroplasts is a temporary product which is hydrolysed, when photosynthesis has ceased, to form sugars which are then either translocated, or used in respiration. To distinguish it from the more permanent starch of storage organs, this starch is described as *transitory*.

In addition to starch, other carbohydrates, such as inulin, and cellulose may be formed from the sugars of photosynthesis.

In those plants which contain fat, this has also been formed from sugar, although the chemistry of the transformation is not certain. It is found, for example, that when oily seeds are ripening, the oil content increases as the sugar content decreases; in the green alga, *Vaucheria*, under conditions in which many plants form starch, oil droplets occur instead.

The formation of proteins involves the utilisation of carbohydrate material formed in photosynthesis, but this will be discussed later (p. 108).

The carbohydrate formation by plants may be represented as follows :



Nitrogen Assimilation

Nitrogen is an essential element for plant growth, and is present in organisms in the form of proteins, which are an important part of protoplasm. It occurs outside the plant in a number of natural forms, constituting about 80 per cent of the atmosphere, and being present in a number of soil compounds.

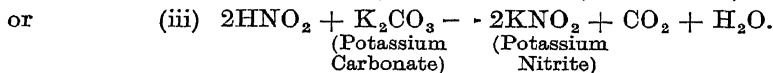
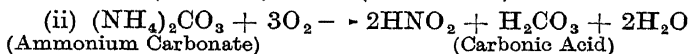
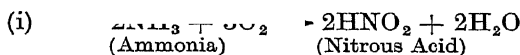
The nitrogenous material of the soil includes organic compounds, or *humus*, derived from the remains of dead plants and animals, and inorganic compounds, such as ammonia and its salts, nitrous and nitric acids, and nitrites and nitrates, especially of calcium and potassium. Of these, the only form utilised by the majority of green plants is the nitrates, although a limited number of plants (e.g. potato) can use ammonia, when necessary. Despite the presence of so much nitrogen in the atmosphere, this is not available to green plants, which, if deprived of nitrates, will soon sicken and die.

Nitrates are extremely soluble, so that, besides being removed from the soil by the roots of plants, they may be lost by drainage. If a soil is to remain fertile, it is essential that its nitrate content shall be continually replenished. The formation of soil nitrate is largely brought about through the agency of minute unicellular plants, the *Bacteria*. Bacteria are of wide occurrence, and all are devoid of chlorophyll. They must, therefore, feed either on substances previously elaborated by plants, or carry out a *chemo-synthetic* process, which takes the place of photosynthesis. The soil bacteria concerned in the production of nitrates include *saprophytic* forms, obtaining their nourishment from dead organic matter, and chemosynthetic forms, which build up carbohydrates from carbon dioxide by obtaining energy from the oxidation of chemical substances.

An important series of processes, carried out by bacteria in the soil, is called *nitrification*, as a result of which nitrates are produced from the organic nitrogen of the soil. The first stage of nitrification consists in the digestion of organic matter, such as dead plant and animal remains, by several *putrefactive bacteria* which include *Bacillus subtilis* and *B. mycoides*. Whilst obtaining food for their

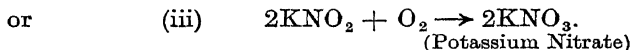
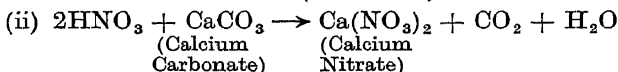
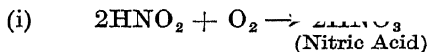
own use, the putrefactive bacteria produce gaseous nitrogen and ammonia, from the proteins of the material which they utilise. The ammonia may remain free, or combine with carbonic acid in the soil to form ammonium carbonate.

Ammonia and its compounds are used as sources of energy by chemosynthetic bacteria, known as *Nitrosomonas*, which oxidise them to liberate energy used by the organism in the formation of carbohydrates from carbon dioxide and water. As a result, either nitrous acid or some nitrite is formed, thus :



The nitrites formed are soluble, but they cannot yet be used by the green plant.

Another bacterium, *Nitrobacter*, is usually present in the soil, along with *Nitrosomonas*. *Nitrobacter* is also chemosynthetic, and oxidises the nitrous acid, or nitrite, formed by *Nitrosomonas*, to obtain energy for the assimilation of carbon dioxide. Its activities result in the formation of nitric acid or a nitrate, the former soon being neutralised, in most soils, to form nitrate, thus :



The nitrates formed are now available for absorption by the roots of plants, but not all of it necessarily enters the roots.

Besides loss from the soil by drainage, nitrates may be lost from badly aerated soils and soils rich in organic manures by the activities of **denitrifying bacteria**. These include *Bacterium denitrificans*, which breaks down nitrates, and other inorganic nitrogen compounds, liberating nitrogen into the soil.

Other bacteria, as well as those of nitrification, are concerned in the maintenance of soil fertility, but play a less important part. Most soils contain bacteria called **nitrogen-fixers**, which develop saprophytically on organic matter. By some means, as yet unknown, these forms utilise the gaseous nitrogen of the soil spaces to build up organic nitrogenous matter in their bodies. This results

in an increase in the organic nitrogen stock of the soil, for when these nitrogen-fixers die their organic matter will be used in the nitrification process. *Azotobacter* and *Clostridium* are nitrogen-fixing bacteria which live free in the soil, the former carrying out its activities in the presence of oxygen, and the latter in the absence of oxygen.

Another nitrogen-fixing bacterium is *Bacillus radicicola*, which can live free in the soil as a saprophyte, but enters the roots of plants of members of the family Leguminosæ, if they are available. It is only a nitrogen-fixer when it has entered the root system of a higher plant. The roots of all members of the family Leguminosæ bear small swellings, or **nodules**, which contain large numbers of the bacterium. The micro-organism infects the root system of its host by way of a root-hair, and having gained entry multiplies rapidly to form a slimy thread-like colony or **zooglea** which spreads from cell to cell in the cortex, which enlarges to form the nodule. It is believed that the leguminous plant provides the bacillus with carbohydrate food, and the bacillus forms nitrogenous material of diffusible nature which is passed on to the cells of the host. When two organisms live in close association, such as this, apparently for mutual benefit, the condition is described as **symbiosis**.

Leguminous plants can absorb soil nitrates in common with other plants, but the presence of *Bacillus radicicola* enables them to grow in soils which would not be satisfactory for most plants, owing to nitrate deficiency. It has been a common agricultural practice for centuries to grow leguminous crops, like beans, clover, vetches and peas, to replenish somewhat impoverished soils. The nodules of the dead roots contain much organic nitrogen which will, in due course, be transformed to available nitrate by the nitrifying bacteria.

The nitrates which enter the green plant are subsequently used in the formation of proteins. Little is known at present about the synthesis of proteins in the plant, but they are built up from simple nitrogenous compounds called amino-acids.

Nitrates are relatively inert substances, so it is thought that, in the plant, they are transformed to a more reactive form. This is followed by a combination, either with carbohydrate or some material formed from carbohydrate, and amino-acids, which invariably contain carbon, hydrogen, oxygen and nitrogen, are produced.

The reaction, in green plants, appears to go on in the leaves, as, owing to their photosynthetic activities, they would provide the necessary carbonaceous matter. The amino-acids formed can be translocated by the phloem of vascular plants to those parts of the plant which require them, either for the formation of protoplasm or to build up protein reserves.

Insectivorous Plants (Fig. 55)

Some green plants supplement their nitrogenous materials by obtaining nitrogen from the bodies of insects. These *insectivorous plants* resemble, in this respect, the carnivorous animals which obtain all their nitrogen from the flesh of other animals upon which they feed.

Insectivorous plants grow in habitats where there is a shortage of nitrates, as for example, in acid peat soils, or situated, as *epiphytes*, on trees where no true soil is present.

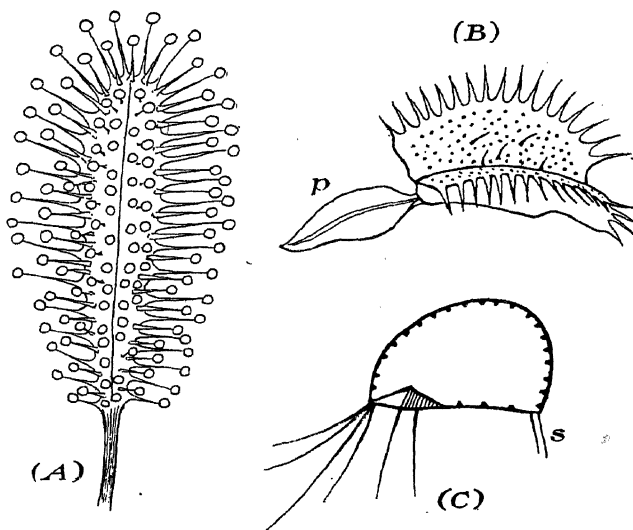


FIG. 55.—Insectivorous Plants.

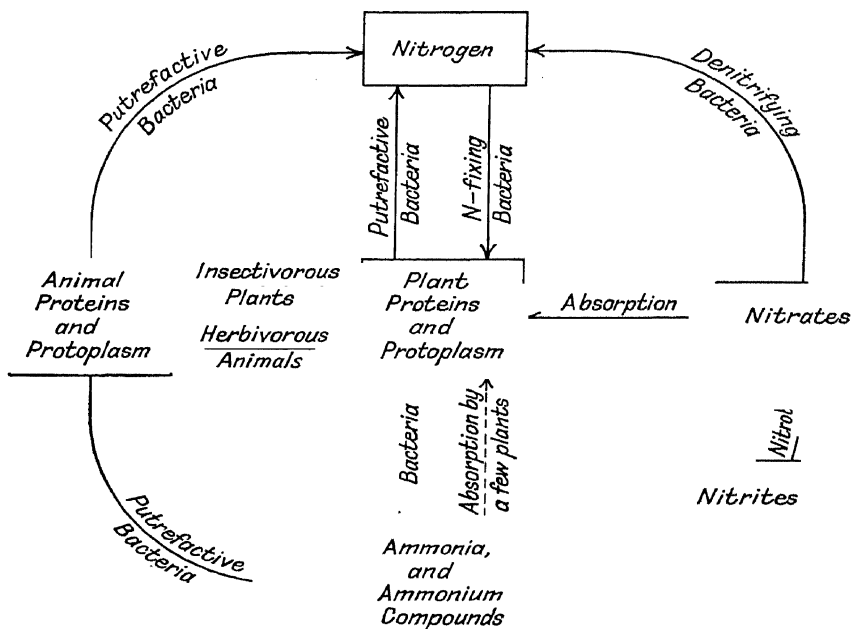
A, leaf of Sundew (*Drosera anglica*) with tentacles expanded ($\times 2$); B, expanded leaf of Venus's Fly-trap (*Dionaea*) ($\times 3$); C, diagrammatic section of bladder of leaf of Bladderwort (*Utricularia*) ($\times 13$).

(p = expanded petiole, s = stalk-like portion of leaf-segment which terminates in the bladder.)

In Britain, three insectivorous genera are found. They are *Drosera*, sundew, and *Pinguicula*, butterwort, growing on damp peat soils, and *Utricularia*, bladderwort, an aquatic plant of acid pools.

The sundew catches insects by means of specialised leaves, the margins of which are drawn out into thin *tentacles*, each terminated by a glistening drop of sticky fluid. The surface of the lamina bears small sticky hairs and digestive glands. When an insect alights on the leaf it is unable to free itself, and the tentacles close over it, bringing it in close contact with the digestive glands. The softer parts of the body are gradually digested and absorbed, after which the tentacles open out again in readiness to capture further insects.

The bladderwort has finely dissected submerged leaves, some of the segments of which are modified into bladder-like traps. The mouth of each trap is covered by a flap which opens inwards only, and sensitive hairs protrude beyond the mouth. The plant grows almost completely immersed in water and when the sensitive hairs are touched by a small water animal the flap opens suddenly. The trap is set by water being lost from it, so that the sides are drawn in. When the flap opens, the tension of the sides of the bladder is relaxed, and water rushes in, owing to the expansion of



the bladder, carrying the water animal with it. Once inside the bladder, the insect cannot escape; it dies and is digested.

The most elaborate insectivorous plants are found in warmer countries. There are several types, but two of the most interesting are the pitcher plant (*Nepenthes*), and Venus's fly-trap (*Dionaea*). *Nepenthes* is either an epiphyte or grows in sterile soils in tropical Asia. It traps insects by means of its leaves, the lamina of which forms a hollowed 'pitcher' above which is a conspicuous broad 'lid.' The upper margin of the pitcher is glossy, and at the lower part of its concavity numerous digestive glands secrete a fluid. Insects are attracted by the bright coloured 'lid,' alight on the

margin of the pitcher and fall into the fluid below. Their bodies are digested and the soluble nitrogenous material is absorbed by the inner wall of the pitcher.

Dioncæa (Fig. 55) is a North American plant, having a rosette of small leaves, each possessing a prominent midrib. The leaf has a round lamina with a toothed margin, and on either side the midrib, on the upper surface, are three sensitive hairs. Insects crawl over the plant, and when they brush against one of the sensitive hairs, the leaf shuts quickly by folding along the midrib. The insect is digested and absorbed, and the leaf may open again.

The diagram on the previous page shows the general circulation of nitrogen in nature, usually referred to as the *Nitrogen Cycle*.

Heterotrophic Plants

Plants may be classed as *autotrophic* or *heterotrophic* according to their method of nutrition.

Autotrophic plants are those which can build up organic food from inorganic raw materials, and include all the green plants which carry out photosynthesis, and the chemosynthetic bacteria.

Heterotrophic plants are devoid of chlorophyll and cannot, therefore, carry out photosynthesis. Consequently they must be provided with organic food, derived, primarily, from that formed by green plants.

Heterotrophic plants may be *parasites*, deriving their nourishment from the tissues of other living plants or animals, or *saprophytes*, which obtain food from the dead tissues of plants or animals, or from non-living organic matter.

The best examples of heterotrophic plants are the Fungi, which are dealt with in Chapter XIII. The heterotrophic habit is found in some higher plants which are undoubtedly degenerate forms derived from autotrophic ancestors.

Several Angiosperms are parasites which attach themselves to other Angiosperm hosts from which they obtain food. Complete parasites do not possess chlorophyll and their leaves are usually reduced to scales, but they carry out the normal method of reproduction by means of seeds. Examples include the dodder (*Cuscuta*), a twining plant attaching itself to the stems of such hosts as the gorse and clover, the broomrape (*Orobanche*), found attached to the roots of clover and ivy, and the toothwort (*Lathræa*), a root-parasite on hazel and alder. The dodder produces small outgrowths, or *haustoria*, which penetrate the stem of the host as far as the vascular tissue, from which nourishment is obtained. The broomrape and the toothwort form root-like haustoria which penetrate the roots, or other underground structures, of their hosts.

A number of Angiosperms are *partial parasites*, for though they attach themselves to host plants, they retain their green leaves and carry out some photosynthesis themselves. A well-known example is the mistletoe, which occurs on the branches of woody plants like the apple and hawthorn. It sends peg-like haustoria into the host, and these elongate year by year to keep pace with the increase in thickness of the branch to which they are attached. Other British partial parasites are common on the roots and rhizomes of grasses, and include the yellow rattle, found in pastures, and the eyebright, found on grassy heaths.

The saprophytic habit is confined to the Fungi, but there are some Angiosperms which are generally said to be saprophytes. These plants occur in soils rich in humus, and have lost their chlorophyll. They appear to be deriving their nourishment from the organic matter of the soil, but closer investigation shows that this is not the case. The true state of affairs is that the underground parts of these so-called saprophytic Angiosperms are infested with a fungus, and it is this which obtains food from the humus and makes it available to the plant. The close association of a fungus with the organ of a higher plant is called a *mycorrhiza*, and is often considered to be an example of symbiosis.

A British example of this type of plant is the bird's-nest orchid (*Neottia*), found in shady woods where there is abundant humus from the fallen leaves. It has a system of short crowded adventitious roots, and a yellow aerial shoot, bearing a few scale leaves, terminated by an inflorescence. The fleshy roots contain the mycorrhizal fungus, and this digests the organic matter of the soil and makes it available to the orchid plant. There is little doubt that in this case the plant would not be able to exist were it not for the fungus, which does not seem to receive much in return.

The presence of mycorrhizas is now known for a large number of plants with typical green shoots. It is possible in these that there exists a symbiotic relationship, as the Angiosperm could pass carbohydrates to the fungus, which might obtain nitrogenous materials from the soil. Orchids can only grow naturally in a mycorrhizal condition, the seed being incapable of forming a seedling unless early infection by the mycorrhizal fungus occurs. Members of the family Ericaceæ, which includes the ling (*Calluna*), heath (*Erica*) and *Rhododendron*, is said to be invariably mycorrhizal, the fungus in some cases being present in the testa when the seeds are shed.

The true relations existing between a plant and its mycorrhizal fungus are uncertain, but views on the part played by the fungus include nitrogen-fixation, and the simplification of organic matter in the soil.

CHAPTER IX

FOODS AND THEIR DIGESTION. ENZYMES

The anabolic processes of green plants result in the formation of food materials, generally in excess of the plant's immediate needs.

These food materials can be regarded as stores of potential energy, as they were primarily formed during the process of photosynthesis, in which light energy is utilised.

Of the foods manufactured by plants, some may be used at once during the respiration of the cells forming them, but the larger surplus is usually translocated to other parts of the plant for use in respiration, for tissue-formation, and for storage in both vegetative organs and seeds. Some of the food elaborated by green plants is used by heterotrophic organisms, such as parasitic and saprophytic plants, and herbivorous animals.

Food may be classified as :

1. Carbohydrates.
2. Fats.
3. Proteins.

Carbohydrates.

Carbohydrates are essential in both plant and animal nutrition. They contain carbon, hydrogen and oxygen, the last two commonly being present in the same proportions as those in which they exist in the molecule of water. They are built up from carbon dioxide and water during photosynthesis, the sugar formed in that process being the source of numerous other organic compounds.

In plants, carbohydrates occur in the cell-wall, in solution in the sap, and as food reserves such as cane sugar, starch, inulin and hemicellulose.

In animals glycogen forms a temporary carbohydrate reserve, and this substance is also found in the Fungi.

The carbohydrates can be classified on the basis of complexity as follows :

- | | | | |
|------------|-------|--|---|
| SUGARS | { | (i) Monosaccharides | (a) Pentoses, e.g. Xylose ($C_5H_{10}O_5$) |
| | | | (b) Hexoses, e.g. Glucose ($C_6H_{12}O_6$) |
| | | (ii) Disaccharides, e.g. Cane Sugar ($C_{12}H_{22}O_{11}$) | |
| NON-SUGARS | (iii) | Polysaccharides | (a) Starches, Inulin, Cellulose ($C_6H_{10}O_5$) _n |
| | | | (b) Gums and Mucilages. |

The *Disaccharides* and *Polysaccharides* are so named because on hydrolysis they yield two or more *monosaccharide* molecules respectively, from which it is believed that they are formed by the condensation of similar numbers of monosaccharide molecules.

Monosaccharides and disaccharides are soluble in water and occur in the cell-sap where their presence results in the development of high osmotic pressures. As their continued accumulation tends to raise the osmotic strength of the sap, it is inconvenient for cells in general to store large quantities of sugar. When storage is necessary, it is usual for other carbohydrates, such as starch and hemicellulose to be formed. Sugars are occasionally found as storage substances, glucose, or grape sugar, occurring in the onion bulb, and sucrose, or cane sugar, in the swollen roots of the carrot and beet.

Of the plant monosaccharides, hexoses are commoner in the free state than pentoses, which are probably derived from them and occur combined in substances like lignin and gums. Glucose is found in photosynthetic tissues which formed it from carbon dioxide and water. It also occurs in other tissues during the digestion of cane sugar, starch and other substances. Fructose is also present in green tissues, and in succulent fruits, and during the digestion of cane sugar and inulin.

Few disaccharides, other than cane sugar, are found free in plant tissues. Maltose occurs in green tissues and in other parts of the plant where starch is undergoing digestion. It is digested to form glucose, and therefore probably represents a stage in the synthesis of starch from glucose which takes place in storage and other cells. In the animal body maltose is formed during the digestion of glycogen, and, as in plants, is ultimately split up to yield glucose.

Polysaccharides are complex carbohydrates regarded as condensation products of simple sugars, which they yield on digestion. The exact composition of their molecules is not known, starch, for example, being represented by the formula $(C_6H_{10}O_5)_n$, where n stands for a number which may lie within 25 and 500.

Starch is the commonest polysaccharide reserve of plants. It may accumulate temporarily in photosynthetic tissues, but occurs more frequently as large grains in the cells of storage organs. Owing to its insoluble nature, starch does not affect the osmotic strength of the cell-sap, and thus forms a convenient carbohydrate to be stored in large quantities. The diversity of form of starch grains was referred to in a previous chapter, but chemically they all consist of two simpler polysaccharides, amylose and amylopectin, together with small amounts of phosphorus and silica in certain plants. When starch undergoes digestion, a polysaccharide,

trin, is formed, which is broken down to maltose and thence to glucose.

Cellulose is another polysaccharide of plant tissues where it forms the typical cell-wall. It has the same formula as starch, but the molecule is composed of a different number of molecular groups, probably about 200. Cellulose differs greatly from starch in its properties, and in the living plant is not usually digested. When it does undergo digestion, a disaccharide, cellobiose, is formed, which ultimately yields glucose.

Hemicellulose forms the thick cell-walls of the tissues of seeds such as the date, lupin, and nux vomica. It is a food reserve, used during the germination of the seed, its digestion products consisting of various hexoses and pentoses.

Inulin is a soluble polysaccharide present in the sap of members of the family Compositæ (e.g. artichoke, *Dahlia*) and in several other plants including the bluebell (*Scilla nutans*). On digestion it yields fructose.

Glycogen is uncommon in plants but does occur as droplets in the cytoplasm of certain Fungi. It is the usual temporary carbohydrate reserve of animals, being found in the liver, muscles, and other parts. It is formed from glucose, and yields this on digestion.

Gums and mucilages are polysaccharides of varying composition, producing, on hydrolysis, hexoses, pentoses and organic acids. Gum arabic is obtained from the stems of *Acacia arabica*, and tragacanth from species of a leguminous genus *Astragalus*. Gums appear to be formed from cellulosic and other cell-walls, either by the activities of bacteria, or by unusual metabolism in the plant.

Fats.

Fats and oils are substances insoluble in water, which occur as food reserves in seeds where they often replace carbohydrate. They are composed of carbon, hydrogen and oxygen, but less oxygen is combined in the molecule than in that of the carbohydrates. Fats are found in some Algæ and Fungi, the perennating stage, or sclerotium, of the fungus, *Claviceps purpurea*, known as ergot, containing up to 60 per cent. Fats may have a significance in plants in producing drought resistance, and, owing to the small amount of combined oxygen in their molecules, they form greater stores of energy than equivalent amounts of carbohydrate.

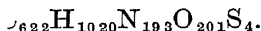
Chemically, fats are esters of glycerol ($C_3H_8O_3$) with certain fatty acids, and are therefore called glycerides. For example, triolein, found in the olive fruit, is the glyceride of oleic acid ($C_{18}H_{34}O_2$). Besides oleic acid, the fatty acids in plants include palmitic ($C_{16}H_{32}O_2$) and stearic ($C_{18}H_{36}O_2$) acids.

The fats of plant tissues are normally fluid at ordinary temperatures, as in the seeds of cotton, flax (linseed), castor oil and ground nut (*Arachis*), but in the cocoa seed the fat is solid, forming 'cocoa butter.'

The origin of fats in the plant is not fully known, but they accumulate in seeds as they ripen, whilst the sugar content falls. This would suggest that they are formed from hexose sugars, which, perhaps, first form glycerol and fatty acid. This is supported by the fact that if an extract of rape seed in glycerol is mixed with oleic acid, fat is formed in the presence of the enzyme lipase (p. 111).

Proteins.

Proteins are complex nitrogenous substances of high molecular weight, which, like that of the polysaccharides, has not been definitely ascertained for any of them. Edestin, a comparatively simple protein found in hemp seeds, has been given the formula



All proteins contain carbon, hydrogen, oxygen and nitrogen, frequently also sulphur, and other elements. Owing to their large molecules they are colloidal, and relatively indiffusible substances. Proteins form an essential part of protoplasm and occur universally as food reserves in seeds, in the form of aleurone grains.

They produce, on digestion, simpler nitrogenous compounds called amino-acids, such as glycine (CH_2NH_2COOH), and alanine (CH_3CHCH_2COOH). These may have been formed in the plant from the sugars of photosynthesis and nitrogenous material from the soil, later yielding proteins which become split up by digestion. Amino-acids are said to be *amphoteric*, which means that they can behave either as acids or bases. The $COOH$ group of one amino-acid may react with the NH_2 group of another, to form a slightly more complex substance. By virtue of the *peptide linkage*, viz. $CO-NH$, it is possible for a number of amino-acids to unite and form a polypeptide. Polypeptides have been made artificially, and found to possess several of the properties of natural proteins, including the *biuret reaction*. This consists in treating an alkaline solution of protein with a few drops of copper sulphate solution, when a violet colour is produced. Polypeptides are formed during the natural digestion of proteins in living organisms. It seems very probable that the synthesis and digestion of proteins involve the same stages, which may be summarised thus:

Protein \rightleftharpoons Proteose \rightleftharpoons Peptone \rightleftharpoons Polypeptide \rightleftharpoons Amino-acid.

Glycosides.

In addition to the true food substances, plants may contain glycosides (= glucosides) which are compounds of sugars with other substances, often of an aromatic nature.

Glucose may be the sugar constituent, but other sugars, both monosaccharides and disaccharides, may replace it, or be present in addition.

Glycosides are usually soluble, and occur in the cell-sap to which they give a bitter taste. They can be hydrolysed to yield their constituents, and, as sugar is thus produced, they have been considered to be accessory food materials.

Evidence of the nutritional value of glycosides is afforded by the willow, in which the glycoside, salicin, accumulates during the day, and disappears overnight when photosynthesis has ceased. It is digested to glucose and saligenin, the sugar being translocated from the leaf whilst the saligenin remains to combine with further sugar on the following day. In the twigs of willow and poplar, the glycoside content increases in the late summer and autumn, to disappear in the following spring during the expansion of the buds.

Most glycosides are harmless substances, but one group, the *cyanophoric* (or *cyanogenetic*) *glycosides* are poisonous to animals as they contain hydrocyanic acid which is liberated on their hydrolysis. Amygdalin is a cyanophoric glycoside found in bitter almond seeds, and prulaurasin is an allied substance in cherry laurel leaves.

Saponins are glycosides which cause the *hæmolysis*, or disintegration, of the red cells of the blood. They include digitonin, found in *Digitalis* leaves, the hæmolytic effect of which is only slight.

Digestion.

The foods of plants and animals are rarely present in a readily assimilable form, so that it is necessary for the more elaborate, and generally insoluble, foods to be simplified before they become available to the living cells. The simplification, or digestion, of foods is brought about, in living organisms, by substances called *enzymes*, produced by the protoplasts for this purpose.

Enzymes are of universal occurrence in living cells, but are, themselves, non-living substances. Their true nature has not yet been elucidated, but much information is available about their characters and activities.

It is possible to extract enzymes from the cells which formed them, and in such a state that they can still carry out their digestive

functions under artificial conditions. The first enzyme to be thus isolated was zymase, which is concerned with the fermentation of sugar solutions by the yeast fungus (*Saccharomyces*). It had been known for many years that yeasts were concerned in the production of alcohol from sugar, but it was not until 1897 that Buchner showed the process to be due to a substance formed by the cells. He mixed yeast with a siliceous earth, kieselguhr, ground them together to destroy the cells, and obtained, from the dead material, a watery extract capable of causing fermentation. The substance responsible for the fermentative activities of yeast was originally called 'enzyme,' but when other substances of a similar nature were discovered, this became a general name, and that of yeast was renamed 'zymase.'

The usual methods for the extraction of enzymes from tissues depend on the fact that whereas protoplasm is killed at 50° C., enzymes are not destroyed until higher temperatures are reached. For example, if germinating barley grains are killed by raising the temperature to 50° C., and mashed in water, the extract obtained contains the enzyme diastase which will digest a starch solution to form maltose. The protein-digesting enzyme, trypsin, can be obtained in a somewhat similar manner from the pancreas removed from an animal.

Enzymes are specific in their action, acting on but one substance or one group of substances. The enzyme invertase digests cane sugar to produce glucose and fructose, but has no action on any other carbohydrate. Maltase, an enzyme often associated with diastase, can digest maltose to glucose, but is also concerned in the hydrolysis of certain glycosides to their components. Trypsin, on the other hand, can carry out the digestion of a great number of proteins, but has no action on any other type of food.

Many enzymes will function only in the presence of a **co-enzyme**, generally of inorganic nature. Pepsin, a protein-splitting enzyme of the stomach, requires the presence of hydrochloric acid, secreted by the stomach for the purpose, and zymase of yeast requires the presence of phosphate.

In some cases cells do not liberate the enzyme produced in an active form but as a **zymogen**, or precursor, from which the enzyme is set free by the action of another substance called an **activator**. An example of such a zymogen is trypsinogen, formed and liberated by the pancreas. Trypsinogen has no action on proteins, but on arrival in the small intestine it is activated by enterokinase, a constituent of the intestinal juice, to set free trypsin which is able to digest proteins.

Enzymes are catalytic in behaviour, for very small amounts are

needed to cause the digestion of large quantities of material, and, at the end of the reaction, the enzyme appears to be unaltered in nature and quantity. They usually act best at an optimum temperature which may vary with the enzyme, the enzymes of the human body having their maximum activity at the normal body temperature of about 37.5° C. Enzymes are destroyed by high temperatures, and by chemical substances such as formaldehyde and mercuric chloride.

There is evidence that enzyme action is reversible, so that the enzymes concerned in the digestion of a substance are also responsible, under different conditions, for the building-up of that substance. Mention has been made earlier in the chapter to the synthetic action of lipase, the enzyme responsible for fat digestion. Lipase may be extracted from rape seeds, and when added to oil will break it down to glycerol and fatty acid. If the ground-up seed containing the enzyme is added to a mixture of glycerol and oleic acid, fat is formed, by the synthetic action of lipase.

In some living cells, enzymes are thought to be associated with *anti-enzymes* produced by the protoplast for protection against the enzymes. If a cell is killed, it usually undergoes *autolysis*, or self-digestion, in a short time, owing to its own enzymes. From this it would appear that, during life, the protoplast remains immune from such enzyme attack, and this immunity may be due to specific substances.

Enzymes are not concerned with the digestion of food materials only. Besides their importance in this connection, they may be concerned with other chemical changes in living cells. It is well known that many living tissues can cause oxidations, for when they are treated with an alcoholic solution of guaiacum resin, in the presence of oxygen, a blue pigment is formed. That the oxidation is due to an enzyme, is shown by the fact that the expressed juice of a potato-tuber will bring about the blueing of guaiacum, but this property is destroyed by boiling either the potato or the extract.

Under natural conditions, the presence of oxidising systems results in the discoloration of tissues following injury, such as occurs with the potato and the broad bean, due to the action of an enzyme, tyrosinase, on the amino-acid, tyrosine.

Recent work on enzyme activity appears to indicate that whenever any chemical process is brought about by living protoplasm it is due to the activity of a specific enzyme.

The following summary includes some of the more important members of the various classes of enzymes :

	Enzyme.	Substance acted on.	Product.
CARBOHYDRASES	Diastase (= Amylase) Maltase Invertase (= Sucrase) Inulase Cytase Cellulase	{ Starch Glycogen Maltose Cane Sugar Inulin Hemicellulose Cellulose	Maltose Glucose { Glucose Fructose Fructose Hexoses Pentoses Glucose
ESTERASES	Lipase	Fats	{ Glycerol Fatty Acids
PROTEOLYTIC ENZYMES	Proteases Peptidases	Protein Polypeptides	Polypeptides Amino-Acids
GLYCOSIDASES	Emulsin = (a) Amygdalase (b) Prunase Salicase Myrosin	Amygdalin Prunasin Salicin Sinigrin	{ Prunasin Glucose { Glucose, HCN Benzaldehyde { Glucose Saligenin { Glucose, KHSO ₄ Oil of Mustard
OXIDASES	Oxygenase Peroxidase Catalase	Catechol { Hydrogen Peroxide or other Peroxide Hydrogen Peroxide	Peroxide Atomic (active) Oxygen Molecular Oxygen
FERMENTING ENZYMES	Zymase (an en- zyme group)	Hexoses	{ Ethyl Alcohol Carbon dioxide

CHAPTER X

PLANT RESPIRATION

Respiration is a process which takes place in all living cells. It is the chief katabolic process, as it consists in the destruction of food materials to liberate the energy contained in them.

Lavoisier, the great French chemist, showed that animals removed oxygen from the atmosphere about them, and gave out carbon dioxide. These gaseous exchanges were, later, found to be connected with the utilisation of food during the activity of the animal. It was subsequently proved that plants effected similar gaseous exchanges, although it was some time before the respiratory exchanges, involving the evolution of carbon dioxide and the intake of oxygen, were distinguished from those of photosynthesis, in which the conditions were reversed.

Respiration is, fundamentally, the combustion of food material in the cell, to set free energy. As all foods contain carbon, a normal product of the process is carbon dioxide. The *intracellular* processes are accompanied, therefore, by gaseous exchanges between the plant and its environment, and as these are the more obvious features, they have usually been considered the essential ones of the process. The vast majority of plants require the presence of free oxygen in order to respire, and under such *aerobic* conditions, they remove oxygen from the air, to which they return carbon dioxide. Although aerobic respiration is necessary for most plants to thrive, particularly if cell-division and movement are to go on, plant tissues will continue to form carbon dioxide for some time after they have been deprived of free oxygen. They are said to carry out *anaerobic respiration*.

Under anaerobic conditions, much less energy is liberated than when aerobic respiration is proceeding. The energy available is insufficient for growth, so that the plant must soon resume the normal method of respiration if it is to continue to grow satisfactorily.

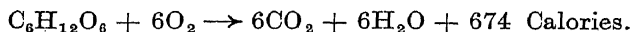
The main features of aerobic respiration, viz. the utilisation of oxygen, the evolution of carbon dioxide, and the destruction of food material, can be demonstrated experimentally. If germinating seeds are placed in a large jar, sealed off from the external air, and left for several hours, at the end of that time it will be found

that the air in the jar will extinguish a lighted taper, and will turn limewater turbid. This indicates that oxygen has been removed from, and carbon dioxide added to, the air in the jar. A similar experiment carried out, either with no seeds, or seeds killed by boiling, would show the atmosphere in the jar to remain unaltered, so proving the changes which take place to be due to the living seeds.

The removal of food material during respiration can be shown by germinating seeds, of known dry-weight, in the dark for several weeks. The air-dry weight of the resultant plants will be found to be less than that of the original seeds. This is due to the fact that, during their time in the dark, the seedlings grow at the expense of the food stored in the seeds, and cannot supplement it by photosynthesis. Some of this food is used to form new tissues, but about half is completely broken down in the respiratory process.

The liberation of energy during the respiration of plant cells is not easily demonstrated. The fact that some of it is dissipated in the form of heat may be used to demonstrate this feature of respiration. Actively growing tissues, such as germinating seeds, or opening buds, provide the best material, half of which must be killed by boiling, and sterilised, with formalin, to prevent bacterial action. The living and dead materials are placed in separate vacuum flasks provided with thermometers, and left for some time. The temperature recorded in the flask containing the living material will be found to be a degree or so higher than that for the killed material, the difference representing heat-energy of respiration.

The food material immediately consumed during respiration is glucose, or another hexose, and the process may be summarised thus :



This equation really obscures more than it indicates, for it suggests that the sugar is directly oxidised, and that the process is the exact opposite to photosynthesis. Neither of these is the case, for, despite the fact that a few Fungi can oxidise sugar directly, it is now known that the hexose sugar undergoes a number of changes before oxygen is utilised, in ordinary plants. Further, in the respiratory process, the reactions occurring are not those of photosynthesis in the reverse order, the intermediate substances differing considerably in the two.

What this equation does show, is that, during the aerobic respiration of carbohydrate food, the ratio $\frac{\text{CO}_2}{\text{O}_2}$ is unity. This ratio is called the *respiratory coefficient*, which is found to vary with

the type of food used in the process. A simple demonstration of the nature of the respiratory coefficient may be made as follows. Two large test-tubes are each fitted with a rubber bung through which the short arm of a bent tube is placed (Fig. 56, A). A little caustic potash solution is placed in one tube, and a little water in the other, and supported on cotton-wool plugs, germinating wheat grains are added to each. The tubes are closed tightly and the free ends of the bent tubes are placed below mercury. After several hours, the mercury will be found to have risen in the tube containing potash, but remains at the original level in the other tube. The rise of mercury in the potash tube indicates that the gaseous exchanges of respiration are going on, and that as oxygen is removed, the carbon dioxide given out is absorbed by the potash,

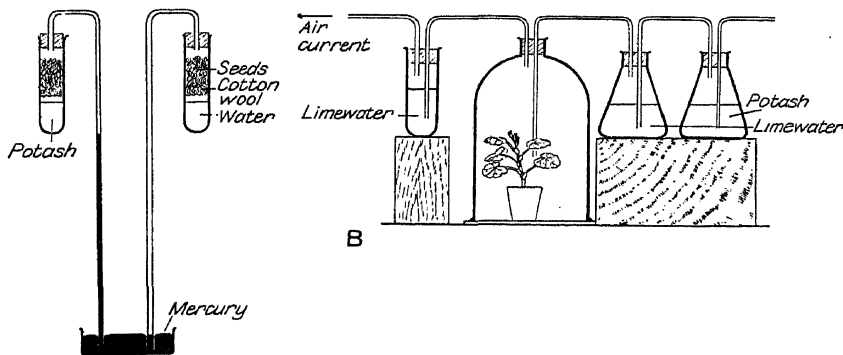


FIG. 56.—Experiments on Plant Respiration (descriptions in text).

A, to demonstrate the respiratory coefficient during the germination of starch-containing seeds; B, to demonstrate the respiration of a green plant. (N.B.—During the experiment light is excluded from the bell-jar.)

causing a decrease in the volume of gas in the apparatus. Similar gaseous exchanges can therefore be assumed to be taking place in the second tube, but as there is no difference in the volume of gas in this tube, as indicated by the stationary mercury, the volume of carbon dioxide evolved must equal the volume of oxygen absorbed, and the respiratory coefficient for starchy seeds is 1.

When complex carbohydrates are used for respiration, they are first digested to the necessary hexose. Cane sugar, starch, and inulin may be the stored foods, and each would be simplified by its specific enzymes. In these cases no energy is set free until the hexose formed is broken down, and consequently the gaseous exchanges of respiration will not commence until then. Therefore the respiratory coefficient, under aerobic conditions, is the same for all carbohydrate foods.

Fats may provide the material for respiration, as in the germination of oily seeds. During the respiration of oily seeds more oxygen is absorbed than carbon dioxide given out, and the respiratory coefficient is less than 1. The following equation indicates the gaseous exchanges in the utilisation of palmitin, the fat of the seed of the oil palm :



It seems probable that, when fats form the food used in respiration, they are first split into glycerol and fatty acids and subsequently, from these, hexose sugar is formed. As fats contain less combined oxygen than do carbohydrates, oxygen would be utilised, prior to respiration proper, in order to effect the transformation suggested. This oxygen absorption, together with that utilised during the combustion of the hexose formed, would account for the greater oxygen consumption during the removal of fats.

In some desert succulents there is an incomplete oxidation of sugar during respiration, and organic acids are formed instead of carbon dioxide. The respiratory coefficient in this case will be 0. During the exposure of these plants to light, the organic acids formed in respiration are broken down to form carbon dioxide, which is then used for photosynthesis.

The anaerobic respiration of plant tissues appears to be of universal occurrence. It consists in the destruction of hexose sugars in the absence of free oxygen, with the formation of carbon dioxide and other substances, including ethyl alcohol (C_2H_5OH).

The process may be summarised thus :



Owing to the fact that the yeast fungus is capable of breaking down hexoses anaerobically to form carbon dioxide and ethyl alcohol, it has been thought that alcoholic fermentation and anaerobic respiration are identical. The fermentation carried out by yeast is known to be due to zymase, which consists of a number of distinct enzymes. Zymase, either in its entirety, or as individual components, has been obtained from a variety of plant and animal tissues. For example, zymase obtained from sugar beet can ferment sugar to form carbon dioxide and ethyl alcohol, in almost the proportions required to fulfil the summary equation above.

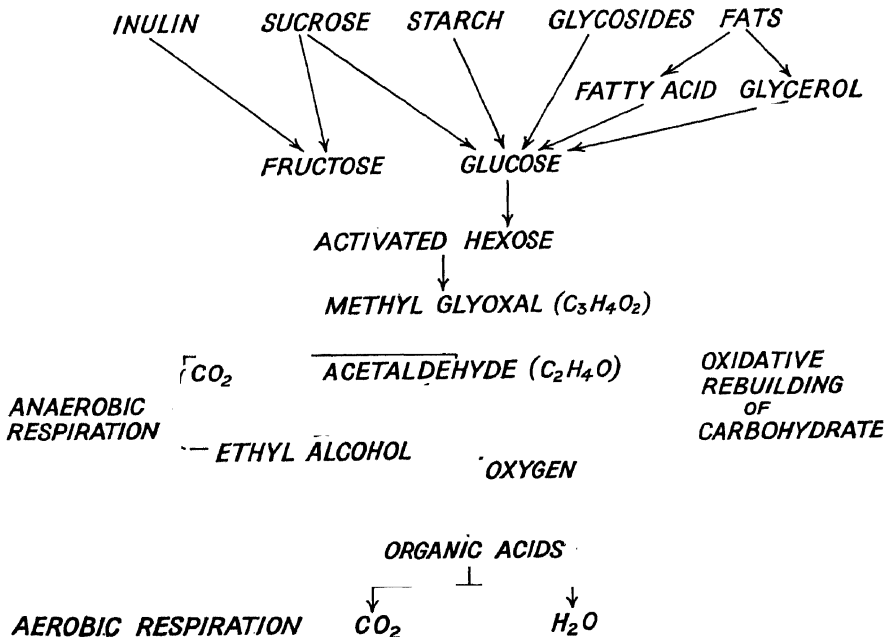
During both fermentation and anaerobic respiration, a number of organic substances have been detected, as intermediate products between the disappearance of the hexose and the formation of carbon dioxide and ethyl alcohol. Some of these intermediate substances have also been detected in tissues carrying out normal

aerobic respiration, which suggests that anaerobic respiration may be the normal precursor of ordinary respiration.

Acetaldehyde is a substance of wide occurrence in respiring tissues, accumulating under anaerobic conditions, to disappear when free oxygen becomes available. Experiments have been claimed to prove that if acetaldehyde is supplied to certain fruits in storage, it is consumed in an oxidative process and energy is set free. This supports the view, now generally accepted, that during respiration sugar is not directly oxidised, but is split up into substances which are subsequently oxidised.

The chemistry of respiration is, at present, largely theoretical, but there is no doubt that the process is much more elaborate than was formerly thought. Further complications arise from the fact, now established for a number of plant tissues, that during aerobic conditions, some of the intermediate products formed in the breakdown of hexose, are not further consumed for energy liberation, but are built up again to hexose, or other carbohydrate, and restored to the plant.

The following summary suggests the processes which may take place during plant respiration :



Respiration and Photosynthesis

As respiration is a characteristic of protoplasm, it will go on in the living cells of all tissues. In the case of green tissues, respiration proceeds simultaneously with photosynthesis, during the day. Under these conditions, photosynthesis is much more vigorous, so that the gaseous exchanges demonstrable are those of this process only. Part of the oxygen formed is used in the cell for respiration, but the greater part is evolved. Similarly, carbon dioxide formed during respiration is used by the green cells in photosynthesis. It is, therefore, difficult to demonstrate the respiration of green tissues when they are exposed to light, but it is possible to show that they carry out the normal process when transferred to the dark.

A green plant (Fig. 56, B) is placed on a greased plate under a bell-jar, into which air, devoid of carbon dioxide, can be admitted and from which the air can be passed through limewater. The bell-jar is covered with a black cloth to exclude light, and air is drawn through the apparatus to remove all carbon dioxide from the bell-jar. After several hours, air is again drawn through, so that the air from the bell-jar passes through limewater. The limewater will become turbid, indicating the formation of abundant carbon dioxide, which has been produced in the respiration of the green plant.

CHAPTER XI

PLANT GROWTH. MOVEMENT IN PLANTS

Growth is a characteristic of living organisms in general, and consists of an increase in size accompanied by the redistribution of available material, such as may be seen during the germination of a seed.

The process requires food, partly to provide the necessary energy and partly for the formation of new protoplasm and cell-walls. Under suitable conditions, plants are capable of continuous growth during life, and this growth consists of an obvious enlargement of the organs. The enlargement of plant organs provides a suitable means of measuring the rate of growth, and of ascertaining the factors which influence it. It is customary to experiment with young plants, such as seedlings, or with immature parts, such as stem and root apices, as it is in these that suitable tissues occur.

In higher plants, such as Angiosperms, growth consists of three phases, viz. (i) the initiation of new cells by meristems, (ii) the enlargement of these cells, by the uptake of water and the addition of new protoplasm, (iii) the differentiation of cells to form permanent tissues.

It is the second phase which causes the enlargement of the plant, and it can be studied by simple experiments.

The region of elongation and the rate of growth of the root can be ascertained by using seedlings with straight primary roots. Equidistant marks with Indian ink are made on the root, from the apex backwards, and the plant is left under suitable conditions for a few days. It will be found that the marks will have separated in certain parts, at the end of this time, indicating both the elongating zone and the amount of elongation (Fig. 57). It is found, by this means, that the elongating region of a typical root extends from the tip to about 5 millimetres behind. It will also be found that, when a particular part has extended to its maximum length, growth is continued by younger parts nearer the apex.

The elongation of the stem is not satisfactorily studied by this method, for it is impossible to mark the extreme tip owing to the young leaves which envelop it. Nevertheless, it is possible to show, by the use of equidistant marks, that the elongating region of the

stem is considerably longer than that of the root, being about 4 to 5 centimetres, in ordinary stems, but up to 50 centimetres in those of twining plants.

An instrument used to record the growth of a primary stem is the *auxanometer* (Fig. 58), which consists of a revolving drum bearing graduated paper against which a pen can move. The pen is attached by a thread to the apex of an elongating stem, in such a way that, as growth goes on, a curve is plotted on the paper carried by the drum.

Growth proceeds only in the presence of certain factors, which are those mentioned in connection with the germination of seeds (Chap. III). The essential factors are, a supply of food, water, free oxygen and a satisfactory temperature.



FIG. 57.—Experiment to demonstrate the zone of elongation in the root of Broad Bean.

A, root with equidistant marks at beginning of experiment; B, after growth has taken place.

Water is necessary both to keep the protoplasm in a suitable state for enzyme and other activities to proceed, and to maintain the turgidity of the cells, which exhibit maximum development in this condition.

Temperature influences all physiological processes, which in their turn may exert some effect on general growth. Growth takes place over a certain temperature range, the minimum being in the region of $0^{\circ}\text{C}.$, and the maximum between 45° and $50^{\circ}\text{C}.$ The general result of an increase of temperature above the minimum up to an optimum between 28° and $37^{\circ}\text{C}.$, according to the plant, is to cause an increased rate of growth. Above the optimum temperature, growth decreases, and ceases completely at the maximum.

Free oxygen is required for respiration, in which energy is set free for growth and other processes. Although most plants can live under anaerobic conditions for a time, they cannot grow unless oxygen becomes available. For example, the yeast fungus may live anaerobically for extended periods, but it is then unable to reproduce itself. On the fungus being supplied with oxygen, it respire aerobically, and liberates sufficient energy for its cells to multiply.

Light is not essential for plant growth, so long as the plant has access to a supply of food material, and is independent of photo-

synthesis. Fungi can develop equally in darkness or light, and seeds can germinate under both conditions. If, however, seeds of plants normally growing under light conditions, are germinated in complete darkness, the plants formed by the end of several weeks

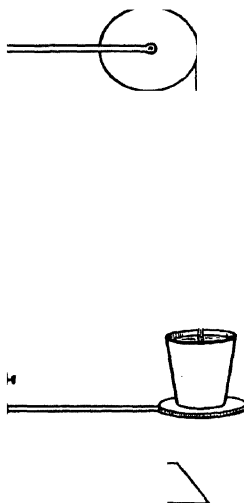


FIG. 58.—Auxanometer, to record rate of growth of an elongating stem, by means of a rotating drum (left of diagram).

present a striking contrast to similar plants grown under natural conditions of illumination. The main differences between the two are indicated in the following table :

<i>Plant in Light</i>	<i>Plant in Dark</i>
1. Sturdy stem with short internodes.	1. Weak, straggling stem with long internodes.
2. Chlorophyll present in leaves and young stems.	2. No chlorophyll developed.
3. Leaves expanded normally.	3. Leaves unexpanded.
4. Tip of stem erect.	4. Tip of shoot hooked as in plumule condition (i.e. in plants such as broad bean and pea).
5. Lateral branches formed by axillary buds.	5. Axillary buds remain undeveloped.

The plant grown in darkness is said to be *etiolated*, because of its drawn-out appearance. Etiolation may be met with under

natural conditions, as when shoots have been accidentally covered by stones, or other objects, and may be induced artificially for commercial purposes, as in the raising of celery and early rhubarb, which are covered to cause the leaf-stalks to become etiolated.

The features of etiolation are not due to lack of photosynthesis, for when plants are grown in continuous red light, partial etiolation occurs, but normal growth goes on in continuous blue light, which is a stimulus to chlorophyll formation.

The amount of light received by an aerial shoot system may have an influence on the anatomical structure of its leaves. Many plants occur naturally in what are known as '*sun*' and '*shade*' forms, and a similar phenomenon may be met in the foliage of large trees such as the beech. The '*sun*' forms of plants and leaves are those exposed to full sunlight, the '*shade*' forms being in such positions as to receive less light. For example, primrose, enchanter's night-shade, and various grasses grow in British woods. When they occur on the outer fringes of the wood they have '*sun*' form, but in the dense shade of the middle of the wood they assume '*shade*' form.

'*Sun*' leaves have a smaller area and thicker mesophyll than '*shade*' leaves, which are said to be due to the harmful effect of strong light on chlorophyll formation. The thicker mesophyll of the '*sun*' leaf is due to two or more palisade layers, the '*shade*' leaf usually having but one layer. In strong sunlight the leaves tend to be set obliquely to the light rays, many of which do not penetrate the mesophyll, but those which do are efficiently absorbed by the more abundant chlorophyll. In the shade, the leaves are so arranged that their laminae are at right angles to the rays and the whole area of the leaf is used in the absorption of light.

Plant Movement

The various organs of rooted plants may display movements which can be either (i) **Growth Movements** or (ii) **Variation Movements**. Growth movements are found only in the younger parts of the plant and are brought about by growing cells.

Variation, or **Turgor** movements occur in more mature parts, and are due to changes in turgidity of the cells of the organ concerned.

Both types of movement can be induced by either external or internal factors. Those movements brought about by external factors are described as **paratonic**, and those by internal factors, **autonomic**.

Paratonic growth movements are most easily studied, as the external factor, or **stimulus**, can be, to some extent, controlled. The stimulus, which may be gravity, water, direction of light and

various mechanical forces, acts in some way on the protoplasts of the responding cells, so that the responses are examples of irritability in plants. In order for movement to occur, the organ must be subjected to the stimulus for a minimum period, called the **presentation time**, and the time which elapses between the onset of the stimulation and the visible response is called the **reaction time**.

The response of plant organs to the stimulus of gravity is known as **geotropism**, and results when gravity is allowed to act unequally on the parts of the responding structure. In erect plants, such as the broad bean, under ordinary conditions a vertical stem and root

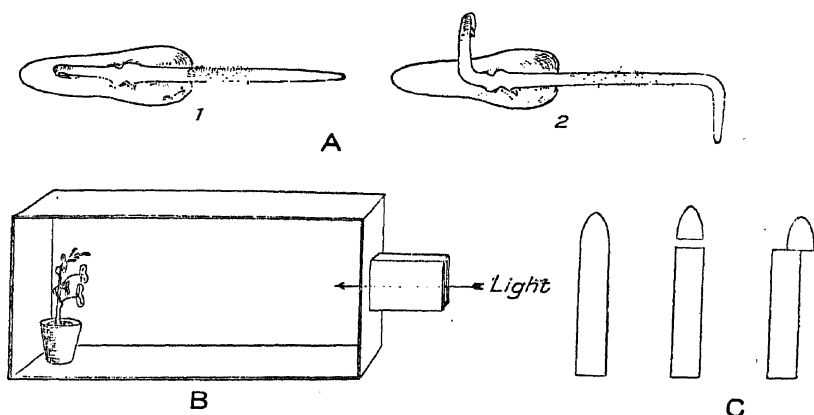


FIG. 59.—Experiments on Plant Movement.

A, geotropic curvature of root and shoot of Broad Bean seedling; B, phototropic curvature of shoot of *Pelargonium*; C, curvature in coleoptile (description in text).

are formed, the former growing upwards and the latter downwards. If the plant is inclined at an angle to the vertical, it will be found that the further growth of its stem and root apices will show a curvature necessary to enable them to grow in the vertical plane again (Fig. 59, A). The stem will curve upwards and the root downwards, being **negatively** and **positively geotropic**, respectively. The stimulus causing this particular response is the one-sided influence of gravity. In the inclined position, one side of the organ is subjected to gravity more than the other, so that curvature takes place by unequal growth of the organ, to set it in such a position that the force of gravity acts vertically through its axis. That this is the case can be demonstrated by means of a **klinostat**, which consists of a drum rotating slowly about its horizontal axis. Seed-

lings with straight stems and roots are pinned in various positions on the drum, so that their axes are at an angle to the vertical. The drum is allowed to rotate for several days, when it will be found that the seedlings have not curved, but have continued to grow along the line they originally occupied. The rotation causes each side of the root and stem to come under the influence of gravity equally, hence the absence of curvature. The majority of primary roots are positively geotropic, and main stems and the erect linear leaves of many Monocotyledons are negatively geotropic. Horizontally growing rhizomes are *diageotropic* (= *plagiotropic*), as their normal position is at right angles to the line of action of gravity. If they are displaced from the horizontal, their growing tips are stimulated to curve into the horizontal position again, by increased growth on one side.

Aerial shoots respond to illumination from one side, the phenomenon being called *phototropism*. This may be demonstrated by placing a young plant with a leafy shoot at the end of a long box which receives light through a slit at the other end (Fig. 59, B). After several days, the tip of the stem will have curved towards the source of light, and the leaves will have tended to set their laminae at right angles to the rays of light. The stem is *positively phototropic*, and the leaves *diaphototropic*.

The roots of many plants are unresponsive to light, but the main roots of the mustard and sunflower are *negatively phototropic*, curving away from the light when illuminated from one side. That the stimulus in phototropic curvatures is the direction of light, causing unequal stimulation of the organ, can be shown by rotating plants with erect shoots on a vertical klinostat in the dark-box used in the last experiment described. Under these conditions no curvature will be brought about, as each side of the shoot will receive equal illumination.

Most ordinary roots respond to the stimulus of water, curving from a drier part of the soil to one in which the water-content is higher. This *positive hydrotropism* may be demonstrated by germinating mustard seeds in a wire-gauze basket suspended so that the contained soil is moister than the surrounding air. In the early stages of germination the emerging radicles will grow vertically downwards in response to gravity, but when they emerge from the soil into the dry air, they curve to remain in contact with the moist soil. This experiment not only shows the response of the root to water, but indicates the fact that when an organ is subjected to two stimuli, one may be ignored whilst the other is responded to.

The curvature in all these tropic movements is due to greater

elongation on one side of the responding organ. A horizontally placed root, for example, must grow more on its upper than its lower side in order to cause the tip to curve downwards.

It can be proved that the part of the organ which perceives the stimulus, is not the elongating zone, but the actual apex, where young cells are situated. If the tip of a horizontal root is removed with a sharp razor, no curvature in response to gravity occurs, and if the tip of an erect plumule is covered with a cap of tinfoil to shield it from light, no curvature in response to one-sided illumination will result.

As the region causing curvature is some distance from the point of perception of the stimulus, there must be some method of conduction of the stimulus in the stimulated organ. There is still much uncertainty as to why the curvature occurs in tropic organs, and a difficult problem is to explain the opposite responses of the root and shoot to the same stimulus in geotropism.

In recent years, evidence has been obtained that the growth of elongating organs, such as stems and roots, is controlled by a substance formed at the apex which diffuses from it to the elongating zone. The substances have been called '*growth-regulators*,' and the name *auxin* given to some of them. One experiment carried out to show the existence of these substances was to cut off the tip of the coleoptile of a barley seedling, and replace it in such a way that only one-half of the stump was covered. As a result the plumule curved by elongating more on the side bearing the tip than on the uncovered side (Fig. 59, c). This was explained as due to the growth-regulator being able to diffuse down one side of the coleoptile, causing the cells of that side to elongate more than those of the side which received no such stimulation.

Other experiments have shown that the growth-regulating substance will diffuse from the severed tips of roots and coleoptiles into small blocks of gelatine, or agar, on which they are placed. When the blocks of gelatine are placed on decapitated roots or coleoptiles, the substance diffuses from the gelatine into the tissue below, and produces the same effects as if the natural tips of the organs were present.

At present it appears that the growth-regulator produced by the root-tip retards growth, whilst that of the stem promotes it.

The responses of the root and stem to gravity might be explained by assuming the growth-regulator to diffuse unequally from the apex of a horizontally placed organ, more diffusing on the lower side. This would result in the greater elongation on the upper side of the root and on the lower side of the stem, which would produce the curvatures known to take place in these two organs. In

phototropic curvature of the stem, it would appear that light retards diffusion on the side illuminated, so causing the greater elongation on the shaded side, resulting in a curvature towards the light.

The movements in the mature parts of organs, due to differences in turgor, can be produced by external factors. An interesting plant which exhibits rapid responses is the sensitive plant (*Mimosa pudica*, Fig. 60), a tropical annual with compound leaves. It closes its leaves in response to various stimuli, which include contact,

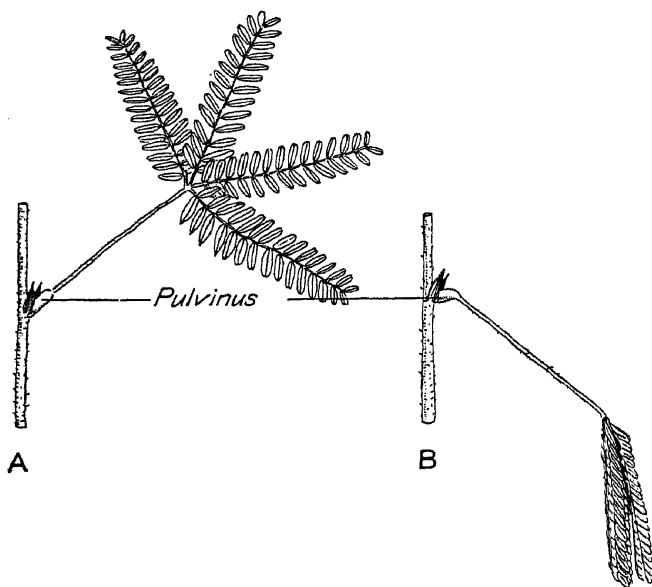


FIG. 60.—Sensitive Plant (*Mimosa pudica*).

A, leaf expanded; B, leaf closed in response to stimulation.

electrical shock, and darkness. When a leaflet of a shoot bearing fully expanded leaves is touched, the leaf quickly folds its leaflets together and droops at the point of attachment to the stem. If the stimulus is sufficiently strong, the leaves of adjacent nodes are also affected, and, in extreme cases, the whole of the leaves of the shoot. The movement is due to the behaviour of the cells of small swellings, or *pulvini*, which are most developed at the bases of the petioles. Each pulvinus consists of much parenchymatous tissue, that on the lower side having thinner-walled cells and a looser arrangement than that of the upper side. As a result of

stimulation, the thin-walled lower cells lose water and become flaccid, so causing the leaf to droop. After a time, the lower cells of the pulvinus regain their turgidity and bring about the raising of the leaf.

The reason for the rapid loss of turgidity is unknown, but experiments suggest that a water-soluble substance diffuses from the point of stimulation and exerts its effect on the responding tissues some distance away.

When the sensitive plant is transferred from light to darkness, the leaves close up, but more slowly than when mechanically stimulated.

A similar phenomenon may be seen in other plants, including the clover, the leaflets of the trifoliate leaves of which close together at night and remain so until the next day. This type of movement is said to be *nyctinastic*.

Motile plants, such as *Chlamydomonas* (p. 130) and other aquatic Algæ, and the spermatozoids of the fern (p. 162) can move in response to a stimulus, the type of movement being described as *tactic*. When a glass vessel, filled with water containing *Chlamydomonas* cells, is illuminated from one side with light of moderate strength, the cells accumulate on the lighted side, but if bright sunlight is used, they swim away from the light to the un-illuminated side. This response is an example of *phototaxis*, *Chlamydomonas* being *positively phototactic* to weak light, but *negatively phototactic* to bright light. When an organism exhibits different responses to the same stimulus, according to its intensity or to other conditions, there is said to be an *alteration of tone*. Other instances of this may occur, as for instance in the geotropic curvature of the flower-stalk of the poppy. In the flower-bud stage, the stalk is positively geotropic and the bud droops, but as the fruit is formed the stalk becomes negatively geotropic and holds the capsule erect.

The spermatozoids of ferns, mosses and liverworts respond to chemical substances produced by the female organs of the plants, and are said to be *positively chemotactic*. The result is to bring the male and female sexual cells in close association for fertilisation to take place. Some motile Bacteria are *aerotactic*, becoming motile in the presence of oxygen, and swimming from a region of low oxygen supply to one where it is more abundant. An example of this was described in connection with the evolution of oxygen during photosynthesis (p. 95).

On considering the various kinds of plant movement, it will be noticed that the responses in general are beneficial to the responding organ.

The positive geotropism and hydrotropism, and occasional nega-

tive phototropism, of main roots, result in their attaining a satisfactory position to carry out their functions of anchorage and absorption. The negative geotropism and positive phototropism of the aerial stem enable it to grow above ground and present its green leaves to the light for photosynthesis.

CHAPTER XII

THALLOPHYTA, 1. THE ALGÆ

Plants are grouped into four large divisions, viz. Thallophyta, Bryophyta, Pteridophyta, Spermatophyta (Appendix, p. 391). The first three form a sub-kingdom, the Cryptogams (or Flowerless-plants), which contrasts with the Spermatophyta in that the members do not form seeds.

The Thallophyta is a large group of simple plants characterised by the absence of a differentiated plant-body or *soma*, and possessing no vascular tissue.

The Algæ form the pigmented group of the Thallophyta, possessing chloroplasts and therefore contrasting with the other group, the Fungi, to which previous reference has been made (p. 103). They are a group of organisms, varying considerably in size and structure, being, for the most part, aquatic or marine, although a few species occur in damp terrestrial situations. The simplest members are *unicellular*, such forms usually being considered to represent the primitive ancestral plant from which the more complex members of our present flora have developed. Other Algæ possess a *filamentous* soma, which may be simple and unbranched, as in *Spirogyra* (Fig. 63), or branched as in *Vaucheria*, a common felt-like growth on soil or plant-pots: *Vaucheria* is somewhat peculiar in its organisation, as the filament consists of a multinucleated cytoplasm enclosed in a common bounding cell-wall, such a structure being called a *cœnocyte*. The highest types of Alga are *thalloid*, possessing a more elaborate multicellular soma, with either a leafy habit, or with an attempt at differentiation to produce a 'stem' with leafy branches, as in *Fucus* (Fig. 64).

The method of growth shows considerable diversity, according to the vegetative structure: the unicellular members undergo division into two; the filamentous forms may elongate apically, when the apical cell, only, is capable of division, or by intercalary growth when each and every cell of a filament may divide; the thalloid forms, such as *Fucus*, elongate and branch by the activity of a special apical cell, and the cells so produced may differentiate along different lines; also, in some thalloid forms a type of secondary growth occurs.

Reproduction in the Algæ may be both *sexual* and *asexual*, the former requiring the fusion of two sexual cells or *gametes*, which produce a *zygote*, the beginning of a new generation. Although in some Algæ there is a regular alternation in the production of asexual and sexual reproductive organs, many of the simpler Algæ appear to carry out both methods irregularly.

The **classification** of the Algæ is somewhat arbitrary owing to the doubts about the inter-relations of the various groups, but a generally accepted classification is based on coloration, although this is accompanied by other characters which are undoubtedly natural.

The *Chlorophyceæ* or Green Algæ possess green plastids containing the four normal pigments, they usually form starch, and possess a cellulosic cell-wall. This group includes *Chlamydomonas* and *Spirogyra*.

The *Phæophyceæ*, or Brown Algæ, are marine plants of an olive-brown colour, due to the presence, in their plastids, of an extra carotinoid pigment, *fucoxanthin*, which masks the green chlorophylls which are also present along with carotin and xanthophyll. The Brown Algæ do not form starch, but other polysaccharides, such as *laminarin*, and their cell-walls are largely pectic, and not pure cellulose. *Fucus* is a member of this group.

The *Rhodophyceæ* or Red Algæ, which are mainly marine, are characterised by the presence of an accessory pigment *phycoerythrin* in their plastids which gives a reddish colour to the plant. Some members also possess a blue pigment, probably *phycocyanin*, and thus are of a purplish colour. They form a granular polysaccharide akin to starch, which gives a red coloration with iodine solution and is called 'Floridean starch.'

The *Myxophyceæ* or Blue-green Algæ, are an unusual group. There is no plastid formation in their cells, but the cytoplasm contains the normal chloroplast pigments along with an additional blue pigment phycocyanin and often a red pigment, said to be phycoerythrin. This group does not carry out sexual reproduction, and an organised nucleus has not been satisfactorily demonstrated in the cell. Blue-green Algæ are frequently the cause of pollution of water.

Chlamydomonas (Fig. 61)

Chlamydomonas is a microscopic unicellular Alga occurring in ponds, ditches and rain pools, where its presence in large numbers results in the green appearance of stagnant water. If a drop of such water is examined microscopically, numerous individual plants will be seen moving rapidly through it, indicating the motility of

the plant, a common feature of many simple Algæ. Each individual consists of an ellipsoidal cell with a minute beak at the anterior end: the protoplast is bounded by a firm cellulose wall through which a pair of fine fibrils of protoplasm, the *cilia*, extend at the anterior beak. The movements of the cell, during which the anterior end moves foremost, are brought about by the rapid lashing of the two equal cilia, which can be seen if the organism is mounted in a weak solution of iodine.

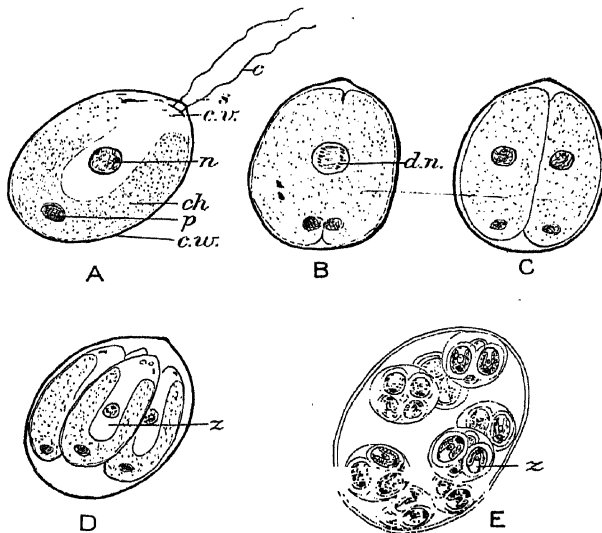


FIG. 61.—*Chlamydomonas*.

A, cell structure; B–D, asexual reproduction; E, *Palmella*-stage (all highly magnified).

(c = cillum, ch. = chloroplast, c.v. = contractile vacuole, c.w. = cell-wall, d.n. = dividing nucleus, n = nucleus, p = pyrenoid, s = eye-spot, z = daughter-cell, to form a zoospore.)

The protoplast consists of clear cytoplasm, in which is embedded a single large basin-shaped chloroplast, situated with its convex surface towards the posterior end of the cell. Within the chloroplast is a darker body, the *pyrenoid*, which consists of a central protein-like crystal surrounded by a sheath of starch grains. The pyrenoid is a feature of the chloroplasts of numerous Green Algæ, and it is thought to be concerned with the synthesis of starch from the sugar produced during photosynthesis. A single nucleus is situated immediately in front of the chloroplast, usually suspended by fine cytoplasmic fibrils.

Close to the anterior beak is a minute red body, the *eye-spot*

or *stigma*, said to be concerned in the perception of light stimuli, and in the same region are two small clear vacuoles, which disappear and reappear with comparative regularity, being called *contractile vacuoles*. The contractile vacuole is probably a mechanism of excretion, although its presence in an organism possessing a cell-wall is not easy to explain.¹

Chlamydomonas is an autotrophic organism, carrying out photosynthesis of a type similar to that of the higher plants. Nutrient raw materials, both mineral salts and carbon dioxide, are absorbed from the surrounding water, where they occur in solution, and the oxygen for aerobic respiration is obtained from the same source.

The organism also exhibits phototaxis. When exposed to diffused light, the cells move towards the source of light, but if bright light is projected on them, the cells tend to move away from it. This response may be of use in the metabolism of the organism, for weaker light is much more useful to cells carrying out photosynthesis than is very bright light.

The reproduction of *Chlamydomonas* may be effected by either asexual or sexual means.

Asexual reproduction (Fig. 61, B) is usually adopted when the organism is well nourished, and is able to carry out satisfactory vegetative growth. A single cell withdraws its cilia and comes to rest; the protoplast, including all the structures present, now undergoes division into two, followed by further divisions of these until four or eight protoplasts have been produced. The daughter-individuals are exact replicas of the original parent-cell, and ultimately acquire cell-walls and cilia. They are liberated by the breaking down of the parent-wall and then commence activities as a new generation. Such motile asexual bodies are *zoospores*, which are commonly produced by many Algæ and Fungi, and vary in size, formation and certain other details.

In certain species of *Chlamydomonas* there is a peculiar variation of the asexual process. The parent protoplast segments to produce daughter-individuals, which, however, are not liberated, and fail to produce cilia. Instead, they form mucilaginous cell-walls and undergo division to form granddaughter individuals, so that a mucilaginous, passive mass of green cells is temporarily formed (Fig. 61, E). This is the *Palmella-stage*, so called because of its similarity to another Alga of that name. The *Palmella-stage* of *Chlamydomonas* is often used as a theoretical basis for the derivation of multicellular from unicellular plants, for if, by some means, this condition had become permanent, it would approximate to a

¹ Contractile vacuoles are common in unicellular animals, e.g. *Amoeba*, and *Paramecium*.

multicellular plant of simple proportions. However, in *Chlamydomonas*, this stage is only temporary and ultimately breaks up to liberate ordinary zoospores.

Sexual reproduction (Fig. 62) usually occurs when conditions

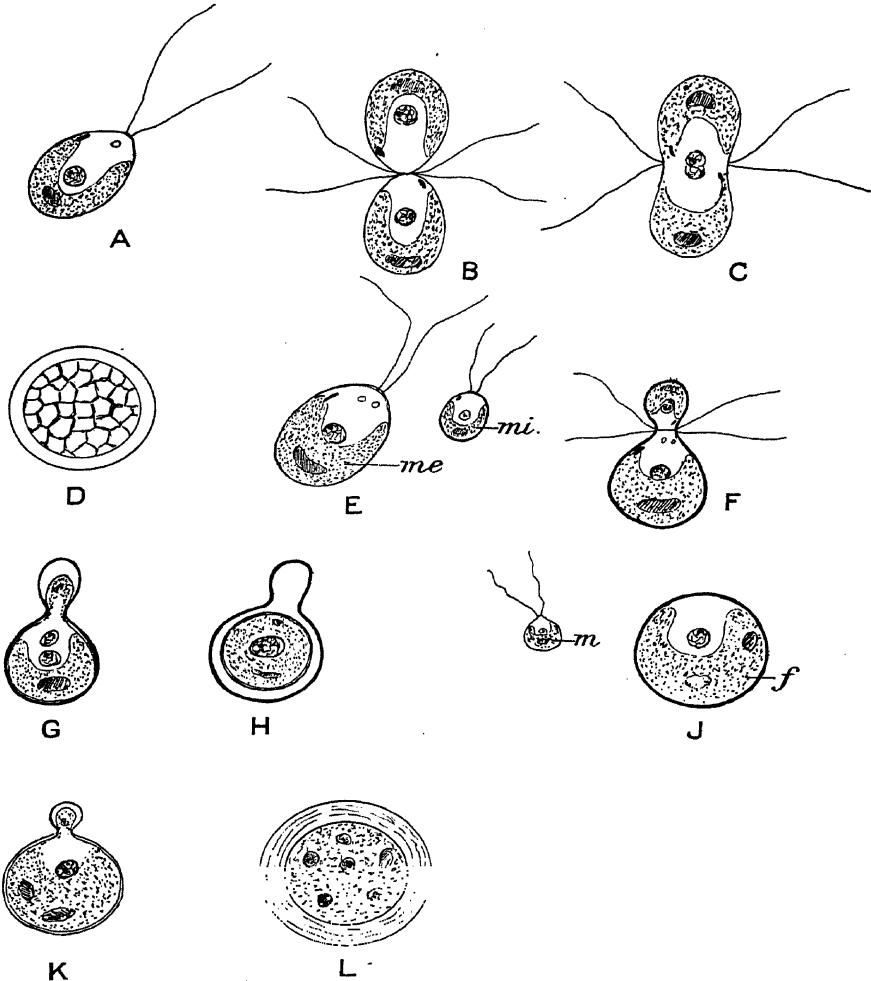


FIG. 62.—Sexual Reproduction of *Chlamydomonas*.

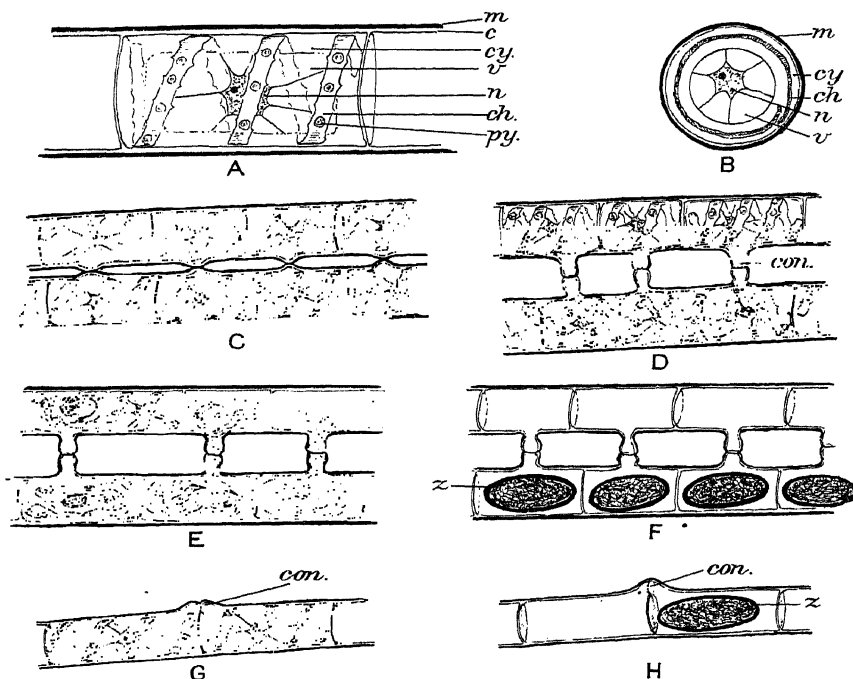
A, gamete of an isogamous species; B, C, conjugation of isogametes; D, zygospore; E, gametes of *C. monadina* (*me* = megagamete, *mi* = microgamete); F, G, H, conjugation in *C. monadina*; J, male (*m*) and female (*f*) gametes of *C. coccifera*; K, conjugation in *C. coccifera*; L, zygospore of same.

are becoming unfavourable to vegetative growth. In the majority of species the cell enters the resting condition, and its protoplast undergoes division, similar to that in asexual reproduction, to form from sixteen to thirty-two small swimmers. The swimmers resemble zoospores except that they may not possess cell-walls on liberation. They swim about for a time, but ultimately meet in pairs. The protoplasts of the swimmers coalesce, and the nuclei of the two unite when this is completed. These fusing cells are gametes, and the cell formed by their union is the zygote. As, in this case (Fig. 62, B), there is no obvious difference in the form or formation of the gametes, they are called *isogametes*, and the sexual reproduction is said to be *isogamous*. After fusion, the zygote transforms the starch it contains to oil, secretes a thick wall and forms a perennating *zygospore* (Fig. 62, D). The zygospore can withstand adverse conditions such as would kill the ordinary vegetative cells. It may undergo desiccation when the pond in which it has been formed dries up, and can be blown away to another situation. When conditions again become favourable to vegetative growth, the zygospore wall is disrupted, and the contents set free. The liberated protoplast may resume its activity as a single cell, but, more often, it divides twice to form four zoospores, which are then liberated to form the new generation.

Although isogamy is common to most species, it is not the only type of sexual reproduction occurring in the genus. In *C. monadina* (Fig. 62, E), the gametes produced are of two sizes, arising by the division of distinct cells. The larger gamete is richer in food reserves and must form the bulk of the resultant zygote. Both gametes are motile. In *C. coccifera* (Fig. 62, J), a single cell loses its cilia and becomes a gamete, whilst another cell undergoes division to form small motile gametes, one of which on liberation fuses with the large passive gamete. Both these examples of sexual reproduction are termed *anisogamous*, but in *C. coccifera* the method is referred to as *oogamy*. It represents the most specialised type of sexual reproduction, in which the large gamete is female, known as an *egg-cell* or *ovum*, and the small motile gamete is male and is called a *spermatozoid*. It is of interest to remember, that in all plants higher than the Thallophyta, oogamous sexual reproduction is the only method used. It is probable that this was evolved from simple ancestral forms, resembling the present species of *Chlamydomonas*, and in the sequence which is here suggested.

Spirogyra (Fig. 63)

Spirogyra is a common Green Alga occurring as a green slimy scum on the surface of still water in ponds, ditches and sluggish streams. It consists of long unbranched threads, composed of cylindrical cells separated by transverse walls, all the cells being alike and completely separated from one another.

FIG. 63.—*Spirogyra*.

A, vegetative cell; B, cell, transverse section; C–F, stages in scalariform (diceious) conjugation; G, H, stages in lateral (monocécious) conjugation).

(c = cellulose cell-wall, ch. = chloroplast, con. = conjugation tube, cy. = cytoplasm, m = mucilage of cell-wall, n = nucleus, py. = pyrenoid, v = vacuole, z = zygospore.)

Each cell is bounded by a cell-wall whose outer layer is composed of clear mucilage and its inner thin layer is cellulose. Within the wall is a lining layer of finely granular cytoplasm in which are seen the characteristic chloroplasts. Each chloroplast is a thin ribbon-like body with an irregular margin, and possesses along its length a number of circular pyrenoids. The centre of the cell is occupied by a large vacuole containing cell-sap, and suspended in

this, by fine threads, or *bridles* of cytoplasm, is a stellate nucleus. The number of chloroplasts per cell varies from one to seven according to the species, and they are spirally wound along the length of the cell.

Elongation of the filament is by intercalary growth, any cell being capable of division. During division the nucleus divides into two, and as the daughter-nuclei separate, a new transverse wall forms between them by a ring-like ingrowth of the longitudinal wall.

Reproduction in *Spirogyra* is either purely vegetative, or sexual.

Vegetative reproduction occurs by the fragmentation of a filament, the transverse walls of some species showing a special development which, on dissolution of the middle lamella, results in the separation of certain cells, to form two distinct filaments.

Sexual reproduction is a special form of isogamy, for although isogametes are produced, they are never set free from the parent filaments.

The common method involves the association of two distinct filaments which become closely cemented along their length by the mucilaginous layers of their cell-walls (Fig. 63, c). The contiguous cells of these filaments commence to form outgrowths from the walls which are in contact, and as these outgrowths enlarge the rest of the filaments are pushed farther apart (Fig. 63, d). The outgrowths continue to enlarge, until the ends fuse and break down to form a short canal or *conjugation tube* (Fig. 63, e). By this time the protoplasts of the conjugating cells have rounded off by slight shrinkage, and one squeezes its way through the tube and fuses with that of the other cell (Fig. 63, e). In this process, the formation of conjugation tubes has usually occurred along the entire lengths of the filaments. Although there is no obvious difference between the two filaments the gametes from one move in the same direction, so that when the process is completed a filament of empty cells is attached to another containing zygotes. It would appear that there is some difference between the filaments of a conjugating pair, because of the behaviour of their protoplasts, and it is permissible to consider the filament which receives the gametes as female, whilst the one which loses its gametes is male.

In some cases three filaments may be involved in conjugation, in which case, two of one sex are associated with one of the other, and all the protoplasts of one filament behave in the same way, in fertilisation.

After the zygote has been formed, it accumulates oily reserves, secretes a thick resistant wall and perennates as a zygospore (Fig. 63, f). The zygospores are liberated by the decay of the

parent-wall, and may survive in much the same way as those of *Chlamydomonas*.

This type of sexual reproduction, involving two distinct filaments, is called **dioecious conjugation**, and, because of the appearance of the two filaments associated by transverse conjugation tubes, is also known as **scalariform conjugation**.

When the zygospore ultimately germinates, the thick wall is broken and a filamentous outgrowth emerges to form the first cell, which, by division, soon produces a new filament. Prior to germination, the zygospore nucleus has divided twice to form four nuclei, three of which disintegrate, the remaining one being the nucleus of the filamentous cell.

In some species of *Spirogyra*, the adjacent cells of the same filament conjugate by means of a tube produced over the separating transverse wall (Fig. 63, G). The resulting zygote gives rise to a zygospore as in scalariform conjugation, so that in such filaments, zygospores will be found in some cells, next to empty cells from which the male gametes have passed. This method of conjugation is called **monoecious** or **lateral**, and may occur in the same species, or even the same filament, that exhibits scalariform conjugation.

Rarely, species of *Spirogyra* commence the formation of conjugation tubes, but before a canal is produced, the protoplasts shrink and form thick walled bodies resembling zygospores. These are called **axygospores** or **parthenospores** and are perennating structures which can later produce new filaments.

Fucus (Fig. 64)

Fucus is a genus of the Brown Algæ, comprising several species which are common seaweeds of rocky British shores where they occupy a zone between the tide levels. The common species are *F. serratus*, *F. vesiculosus* and *F. spiralis*, the two former being dioecious with male and female organs on distinct plants, whereas the latter is monoecious as the same plant bears both male and female organs.

The plant body of all species is a flattened structure, or thallus, of moderate size, reaching several feet in length in older plants. The thallus is multicellular and exhibits a simple division of labour, indicating a higher specialisation than in the Green Algæ described. It consists of an elongated stalk, the **stipe**, firmly attached to a rock, or large pebble, by a discoid holdfast or **hapteron**. At the free end it bears a series of flattened forked branches, the **frond**, each branch of which shows a distinct **midrib** and thins out at the margin to two lateral '**wings**.' The thallus, therefore, has the

superficial appearance of an attached leafy shoot, and although the holdfast and stipe cannot be assigned definite physiological functions, there is no doubt that the expanded frond is an effective photosynthetic system.

The whole thallus is of a brown colour, due to the presence of *phæoplasts*, or chloroplasts containing the four normal chloroplast pigments together with fucoxanthin, which occurs in greater proportion than the other carotinoids. The presence of chlorophyll

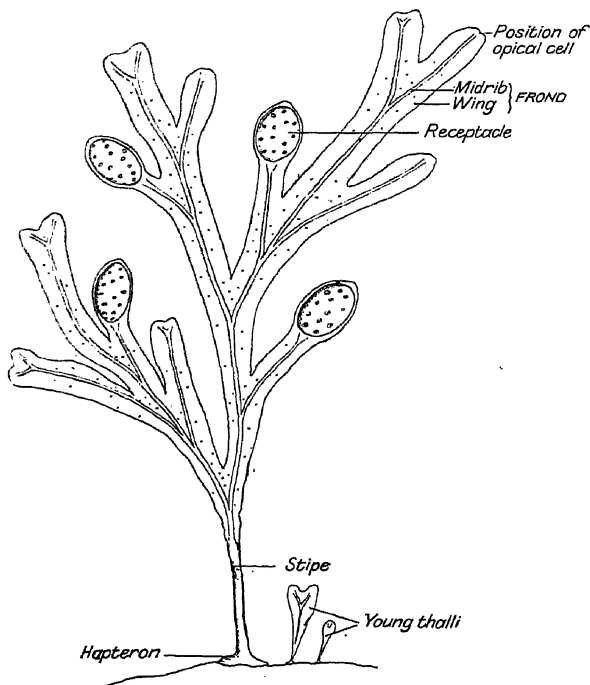


FIG. 64.—Thallus of *Fucus spiralis* [$\times \frac{1}{4}$].

may be demonstrated by dipping the thallus into boiling fresh water, when a vivid green colour results.

The elongation of the thallus is brought about by the division of an apical cell, situated in a depression at the tip of each branch. This apical cell cuts off cells by walls parallel to the inner walls to cause both elongation and widening of the frond, and, at more or less regular intervals, divides longitudinally to produce two cells which both remain meristematic and become the initials of new branches. It is by this latter division that the characteristic

forking or *dichotomous branching* occurs. The thallus not only has a morphological differentiation, but also exhibits an internal structure of somewhat elaborate type. If a transverse section of the frond (Fig. 65, A) is examined, several zones of tissue can be

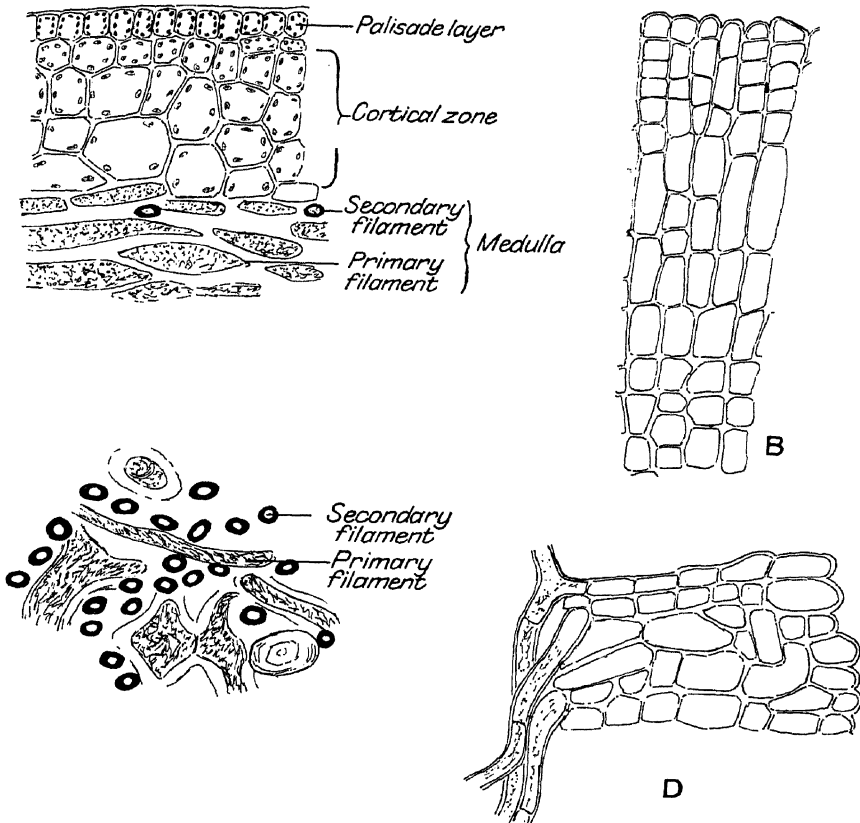


FIG. 65.—*Fucus*.

A, transverse section of part of frond of thallus; B, transverse section of part of stipe showing secondary growth of cortical cells; C, transverse section of medullary zone of stipe; D, longitudinal section through part of base of stipe showing secondary medullary filaments formed by cortical cells.

seen. The outer surface layer consists of compact *photosynthetic cells*, each containing numerous phaeoplasts, and acts as an epidermis, as well as being the main photosynthetic tissue of the plant.

Below the bounding layer is the *cortex* consisting of several

layers of larger cells with thinner walls and containing fewer plastids. The central zone of the thallus consists of filamentous cells forming the *medulla*. In the mid-rib the filaments run longitudinally, but branches pass out laterally into the central part of the wings. The medullary filaments consist of elongated cells with clear mucilaginous walls, the transverse walls often having the appearance of sieve-plates of vascular plants. The medulla is considered to be concerned in the transport of food materials formed in the upper well-illuminated part of the thallus, to the lower regions where photosynthesis is not likely to occur. Examination of the stipe shows it to be the central part of a former frond, the wings of which have died and been shed as elongation of the thallus proceeded. The bulk of the stipe, therefore, represents a former mid-rib, but as it is now much thicker than the mid-ribs of the existing fronds, some method of thickening has gone on. The increased girth of the mid-rib is brought about by a specialised type of secondary growth, in which the cortical cells are concerned. The middle layers of the cortex divide tangentially to increase this tissue (Fig. 65, B), whilst the innermost cortical cells give rise to long cells which pass, as filaments, amongst the cells of the medulla (Fig. 65, C). The *secondary medullary filaments* may be distinguished from primary filaments by their thinner walls.

The holdfast also grows in area with age, in order to keep pace with the additional strain of the increasing frond. The increase is accomplished by cortical activity, some of the secondary medullary filaments passing downwards to expand against the rock surface (Fig. 65, D).

Fucus is autotrophic, absorbing its nutrient materials from the sea and carrying out photosynthesis by means of its chlorophyll-containing plastids. Brown Algæ, in general, exhibit a selective absorption of iodine, which is present in almost imperceptible amounts in sea-water but occurs in such proportions in the Phæophyceæ as to form a commercial source of the element. The part which iodine plays in the plant is obscure, but as it combines with fucoxanthin, this would explain its continued absorption, because of the removal of free ions.

Respiration is aerobic, oxygen being obtained from that dissolved in the surrounding water. There may be some difficulty of aeration of the inner tissues as the thallus of *Fucus* is characterised by the lack of intercellular spaces. *Fucus vesiculosus* possesses pairs of air-vesicles, formed by local disorganisation of the central tissue of the thallus. These vesicles act mainly as air-floats, to buoy up the thallus when it is submerged.

The reproduction of *Fucus* is by sexual means only. It may

PLATE IV

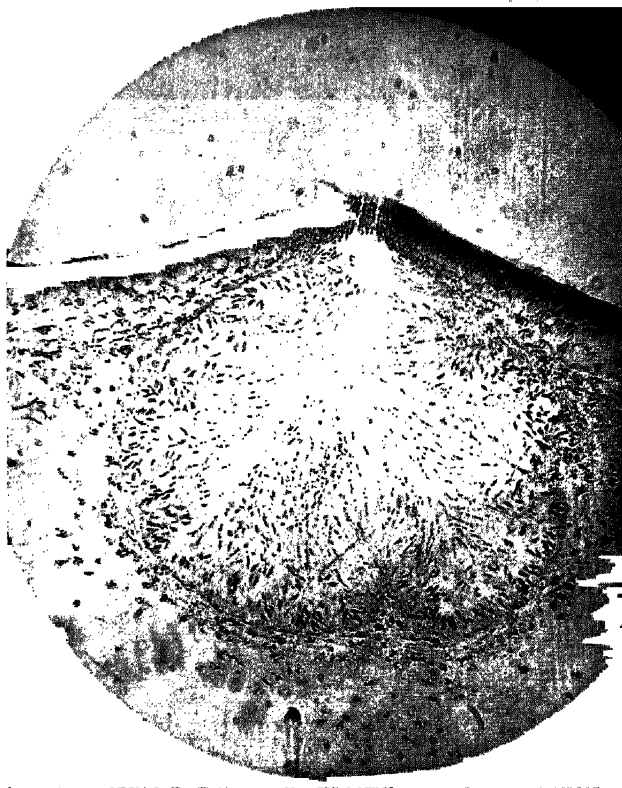


FIG. 66.—Photomicrograph of a longitudinal section of the male conceptacle of *Fucus serratus*.

The darkly-stained cells in the conceptacle are the antheridia.

sometimes be found that 'buds' have arisen on wounded surfaces of older thalli which are healing, but there is no evidence that a detached piece of a thallus can form a holdfast and become a new plant. The gametes are produced by special apical branches which are more swollen than the other part of the frond. Each fertile branch, or *receptacle*, bears a number of cavities, or *conceptacles*, which communicate with the surface through small pores, or *ostioles*.

Fucus serratus and *F. vesiculosus* produce male and female receptacles on distinct plants, which though morphologically similar can be distinguished, when fertile, by an orange slime on the male receptacle and an olive-green slime on the female.

In transverse section, the male conceptacle of *Fucus serratus* (Fig. 66), is seen to be lined with cells, some of which give rise to multicellular filaments projecting into the cavity. These filaments are either unbranched or branched. The unbranched filaments are sterile *paraphyses*, some of which may pass through the ostiole. The branched filaments bear the male organs, or *antheridia*, which are swollen cells at the ends of some of the branches (Fig. 67, c). Each antheridium arises from a single cell, the nucleus of which undergoes division, followed by further division of the daughter-nuclei, to form sixteen or more small uninucleate spermatozooids.

The female conceptacle (Fig. 67) possesses paraphyses like the male, but the female organs, or *oogonia*, are large elliptical cells, attached by short unicellular stalks to the lining of the conceptacle (Fig. 67, b). The oogonium originates as a single cell which enlarges and undergoes division to form eight egg-cells. Each egg-cell is a spherical body, several thousand times larger than the spermatozooids, and containing numerous discoid phaeoplasts which give it an olive-green colour.

The gametes are usually set free when the thalli are exposed to the air at low tide and some shrinkage occurs.

The walls of the antheridium and oogonium consist of several layers, the outer of which is first ruptured to liberate the sexual organ, with its contents, into the cavity of the conceptacle. From the conceptacle, the sexual organ is extruded through the ostiole to the surface of the thallus, where rupture of the remaining layers of the wall sets free the gametes, which lie in a film of mucilage on the receptacle.

The male and female gametes are washed from the thallus when the tide rises. The spermatozoid is now seen to be a minute pear-shaped cell with a small orange chromoplast, eye-spot, and a pair of laterally placed cilia (Fig. 67, d). The egg-cell is quite passive, but spermatozooids are attracted to it and congregate at its surface.

A single spermatozoid ultimately penetrates into the cytoplasm of the egg-cell and effects fertilisation, which is oogamous. The spermatozoids around the egg, which are not successful in effecting fertilisation, move away to other unfertilised egg-cells.

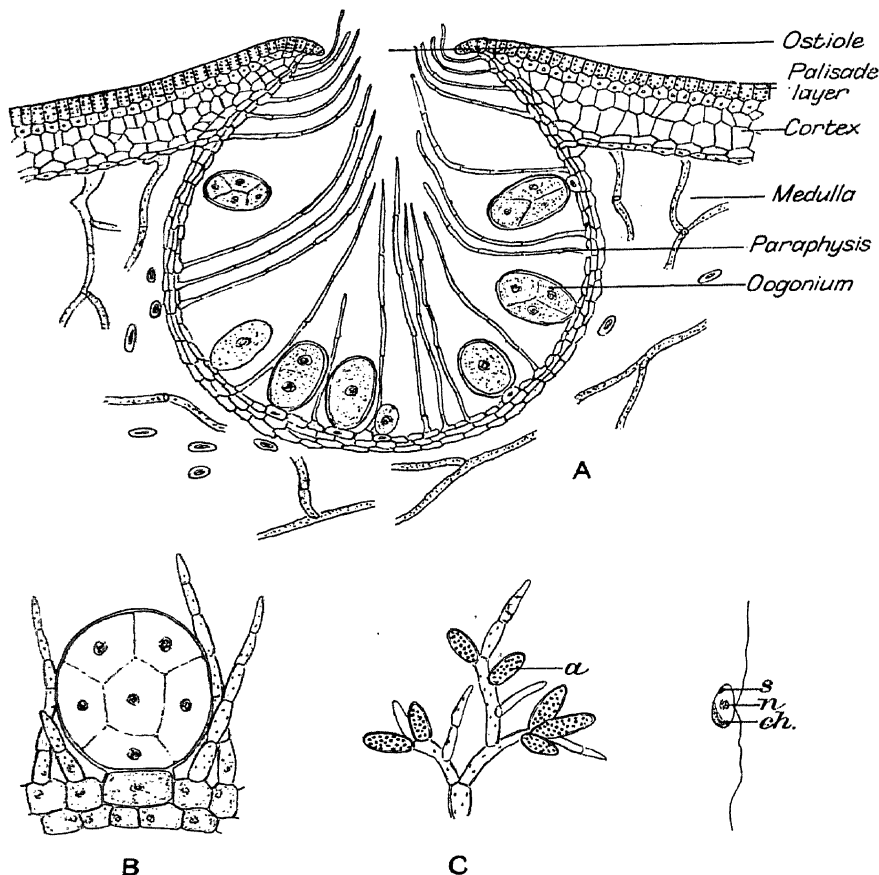


FIG. 67.—*Fucus serratus*.

A, longitudinal section of female conceptacle; B, single oogonium, with adjacent paraphyses; C, branched filament from male conceptacle bearing antheridia (a); D, spermatozoid (ch. = chromoplast, n = nucleus, s = eye-spot).

After fertilisation the zygote sinks to the sea-bed, secretes a cell-wall and commences to develop immediately. The absence of a resting period, comparable with that of the zygospores of *Chlamydomonas* and *Spirogyra*, is probably connected with the more uni-

form conditions which prevail in the sea, compared with the seasonal changes in inland waters.

The zygote first divides transversely into two, the lower cell being the commencement of the holdfast, and the upper cell the commencement of a simple frond. By continued division a small plant is formed with the discoid holdfast and thallus terminated by an apical cell. Several years elapse before this plant is capable of forming gametes.

The reproduction of the other species of *Fucus* is similar in general details to that of *F. serratus*. In *F. spiralis*, however, antheridia and oogonia occupy the same conceptacle. They are of the same type as those of the dioecious species, and also produce gametes which effect fertilisation after liberation from the conceptacle to the surface of the thallus.

CHAPTER XIII

THALLOPHYTA, 2. THE FUNGI

The Fungi are plants of simple structure characterised by the absence of chlorophyll. They are grouped with the Algæ because of the absence of differentiated tissues, but the two divisions of the Thallophyta differ greatly in their methods of nutrition. The origin and relationships of the Fungi are matters of controversy, some authorities holding the view that they have descended from Algal ancestors, whilst others consider them to have evolved independently from Protist ancestors which never possessed chlorophyll.

Fungi agree with other plants in the possession of cell-walls which permits them to take up fluids only. The cell-wall, however, often differs from that of typical plants, in that it is not composed of pure cellulose, but contains nitrogen and resembles the chitin of certain animal investments.

On account of the lack of chlorophyll the Fungi are heterotrophic, obtaining food material in an elaborated form either parasitically or saprophytically. Despite their simple structure, Fungi are of considerable interest from a physiological point of view. Saprophytic forms play an important part in bringing about the decay of organic matter, and it is largely by their activities that dead matter does not accumulate, although they are assisted in its destruction by the Bacteria. Saprophytic fungi are also responsible for fermentation, which is of commercial importance in baking and brewing, and for the ripening of cheeses, like Stilton and Gorgonzola, which is effected by species of Blue Mould (*Penicillium*).

Parasitic Fungi may be of economic importance when they select cultivated plants for their hosts. Black rust of wheat, and some other cereals, is due to *Puccinia graminis*, and potato blight is caused by *Phytophthora infestans*, and the attacks of both may be so severe as to damage the crops and cause considerable monetary loss. *Claviceps purpurea* is a fungal parasite on rye and other grasses, infecting the ovary of the young flower and replacing it with a compact fungal growth called a *sclerotium*. This sclerotium is the 'ergot' used in pharmacy and medicine.

The nutritional activities of the Fungi are connected with their enzyme production. Saprophytes simplify complex organic foods

by the secretion of enzymes, whilst parasites often gain an entry into the tissues of the host by digesting their way through the epidermis and other tissues.

Such saprophytes as the Blue Moulds can grow on a wide variety of organic media, and must possess the specific enzymes for the digestion of each. *Penicillium glaucum* can obtain nourishment from starch, inulin, glucose, proteins, fats and other substances, and produces the enzymes required for their digestion.

The enzyme, diastase, is obtained commercially by culturing the mould *Aspergillus Oryzæ* on rice bran and extracting the enzyme with water.

The nutrition of many Fungi is not clear, for various species have been found to develop in such liquids as copper sulphate solution, sulphuric acid, and arsenical solutions in which organic matter does not occur.

The vegetative body of a fungus is called the *mycelium*, and is generally composed of fine filaments, or *hyphæ*, which may possess transverse walls. The hyphæ elongate apically and branch extensively to form either a loose network, as in the moulds, or a more compact *pseudo-parenchyma*, as in the reproductive portion of the mushroom.

Fungi are classified mainly on the basis of spore-formation into three big groups. The Phycomycetes (e.g. White Moulds) have a structure and types of reproduction similar to some Algæ. The Ascomycetes (e.g. Blue Moulds) form a characteristic sporing-body called an *ascus*, which contains *ascospores*. The Basidiomycetes (e.g. Mushroom) abstrict spores externally from a special club-shaped cell called a *basidium*.

Mucor (Fig. 68)

Mucor is a genus of White Moulds occurring abundantly on many organic substances, such as bread, fruit, cheese and other materials. All the species are saprophytes, and a culture can be obtained by exposing a damp piece of bread to the air for a few days, when it will be found to be covered by an extensive growth of fine white threads. This growth is the mycelium of *Mucor*,¹ consisting of a tangle of hyphæ which may form short branches penetrating the nutrient material which is soon digested to a pulpy mass. Each hypha is bounded by a rigid cell-wall, lined on the inside with cytoplasm, in which numerous small nuclei occur. The centre of the hypha is occupied by a vacuole, which is continuous along its length,

¹ A fungus, *Rhizopus nigricans* (= *Mucor stolonifer*), may be found on damp bread. In all its general features it is identical with *Mucor*, and may be used for study.

and also with the vacuoles of the branches of the hypha. There are no transverse walls in the vegetative hyphæ, and as the nuclei are found in a common cytoplasm, the structure is a cœnocyte. Owing to the presence of numerous nuclei, each representing a potential cell, the cœnocyte must be considered as equivalent to a multicellular structure.

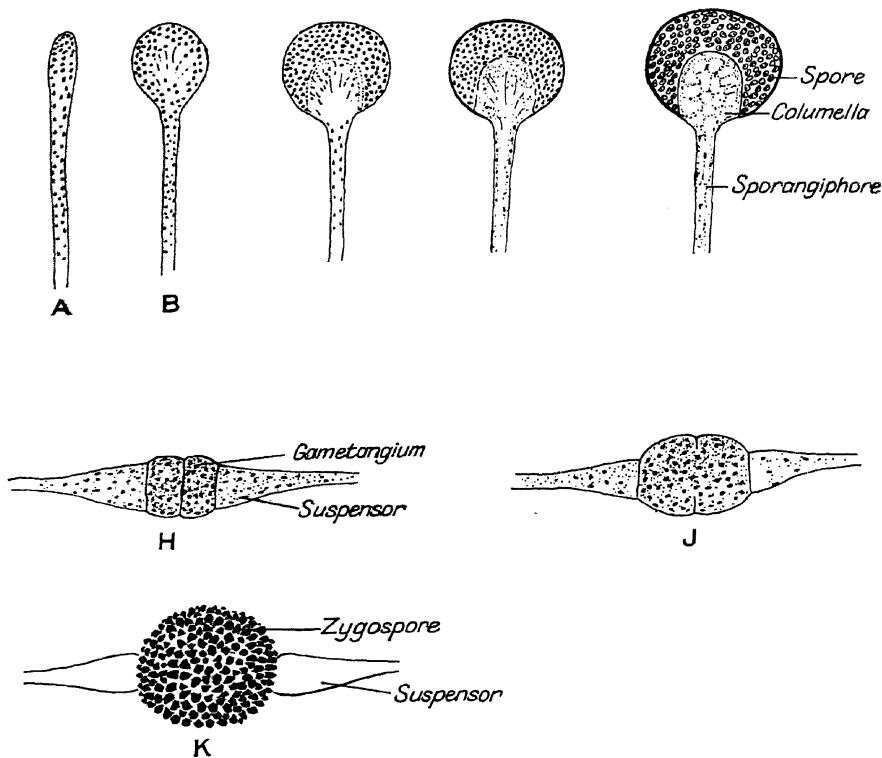


FIG. 68.—*Mucor* (much enlarged).

A-E, development of asexual sporangium (description in text); F-K, sexual reproduction (description in text).

The hyphæ spread by apical growth over the surface of the medium they occupy, and the branches arise as simple outgrowths behind the tip, as it advances.

The common method of reproduction is asexual, which takes place when the fungus is growing actively under suitable conditions of food-supply, water and temperature. The mycelium gives rise to erect branches, the tips of which accumulate a dense mass of cyto-

plasm containing many nuclei (Fig. 68, A), brought about by a protoplasmic streaming from below. The tip of each branch commences to swell, and the nuclei arrange themselves towards the periphery, leaving a clearer region in the centre, where small vacuoles appear (Fig. 68, C). A dome-shaped cleavage-plane now develops at the top of the stalk of the swelling, between the outer nucleated region and the central clear zone. The cleavage plane is replaced by a thin wall, completely isolating the nucleated cytoplasm from the rest of the hypha (Fig. 68, D). Meanwhile, the cytoplasm of the swollen tip has divided to form a number of angular masses, each surrounded by a cell-wall and containing two or more nuclei (Fig. 68, E). In this way the asexual *sporangium* is formed at the apex of an erect *sporangiophore*. The central sterile part of the sporangium is called the *columella*.

It should be noted that the so-called spores of *Mucor* differ from true spores, such as the zoospores of *Chlamydomonas*, and fern spores, in that they are multinucleate bodies, whereas true spores are typically uninucleate.

The wall of the sporangium bears a deposit of calcium oxalate on its surface, and when ripe is comparatively brittle. The spores are released by the bursting of the wall which is assisted by a swelling of the columella. The minute spores are carried in the air, from which they may ultimately settle on suitable organic material for germination to proceed.

Mucor can reproduce itself sexually, but this method is much less common than by asexual means, for it requires two distinct mycelia to come into close association for it to occur. When hyphæ of the two necessary mycelia become associated, the apices of creeping branches grow towards one another and finally meet (Fig. 68, F). The tips, which contain multinucleate protoplasm, commence to swell, and are cut off from the rest of their respective hyphæ by a transverse wall (Fig. 68, H). The associated tips then fuse, or *conjugate* (Fig. 68, J), which is a fusion of gametangia (sexual organs) and not of gametes, which are represented by the individual nuclei. The nuclei subsequently fuse in pairs (one nucleus from each hypha), inside the fused gametangia, the fusion nuclei strictly being equivalent to the zygote nuclei of other plants.

Enlargement continues until a globular structure, or 'zygospore,' is formed, which has a thick dark warty coat, and is able to perennate for long periods (Fig. 68, K). The 'zygospore' of *Mucor* differs from that of *Spirogyra*, or *Chlamydomonas*, as it does not represent the fusion of a pair of gametes, but of numerous pairs of gametes. When the zygospore subsequently germinates, the thick coat splits and an erect sporangiophore is formed, which is identical

with that described above. The spores are dispersed and continue to form vegetative mycelia.

The complicated sexual reproduction of the White Moulds, or Mucorinæ, was discovered by Blakeslee in 1904, using in the first instance, *Rhizopus*, a species allied to *Mucor*.

Blakeslee found that the conjugating mycelia were alike in general appearance and could only be distinguished by their sexual behaviour. He designated the two forms + and — strains, and showed that zygospores were only formed when a hypha of the + strain was associated with that of a — strain. A pure culture of one or other strain could not, on its own, form zygospores.

Those fungi, including *Mucor*, which require the fusion of distinct mycelia in sexual reproduction, are said to be *heterothallic*.

The sexual reproduction is still considered to be isogamous, as the gametes are identical in formation and appearance, so far as can be seen at the present time.

The Mushroom Fungus (*Psalliota campestris*¹)

The mushroom fungus is a well-known plant growing naturally as a saprophyte on the humus of grassland, and being extensively cultivated on a commercial scale, on rich organic soil.

The mycelium consists of a tangle of white hyphæ which may become interwoven to form coarser threads, or *rhizomorphs*. The hyphæ are septate, i.e. possess transverse walls, and the various segments contain two or more nuclei.

The fungus obtains all its nutrient material from the soil, digesting the organic matter of dead plant remains, and absorbing water and salts also.

Under natural conditions reproduction is carried out either by the spread of the mycelium vegetatively, or by means of large spore-bodies, or *sporophores*, the familiar mushrooms. The sporophore arises from a small mass of interwoven hyphæ immediately below soil level (Fig. 69, A), the component hyphæ growing rapidly to form a small oval swelling which emerges from the soil. This young sporophore continues to grow, and by local inequalities of growth and some specialisation of hyphæ, produces a swollen structure with a transverse constriction (Fig. 69, B). The inner tissue consists of elongated branching hyphæ, and the outer of a protective skin or *veil*. The upper part of the sporophore expands laterally, and forms an annular cavity into which specialised hyphæ, with binucleate

¹ Formerly *Agaricus campestris*. The genus *Agaricus* used to include a large number of fungi which have now been divided amongst several genera. These genera are included in the family Agaricaceæ, commonly called Agarics, or Gill-fungi.

segments, grow vertically downwards to form plates of tissue (Fig. 69, D). The lower part of the sporophore becomes somewhat elongated as a cylindrical stalk, or *stipe*, which bears a now-expanded dome-like cap, or *pileus* (Fig. 69, E).

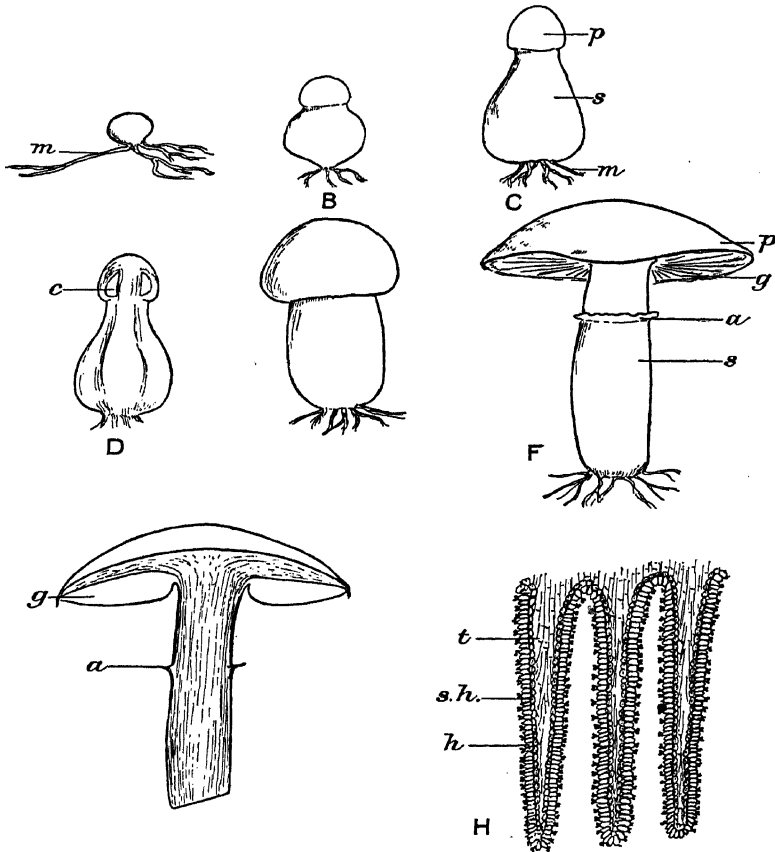


FIG. 69.—Mushroom Fungus (*Psalliota campestris*).

A-G, stages in development of sporophore (D and G, longitudinal section); H, longitudinal section of gills [$A \times 1$, B-G $\times \frac{1}{2}$].

(a = annulus, c = cavity in which gills form, g = gills, h = hymenium, m = mycelium, p = pileus, s = stipe, s.h. = sub-hymenium, t = trama.)

The downgrowths into the cavity of the pileus are spore-forming plates, the *lamellæ* or *gills*, which are finally exposed by the lateral expansion of the pileus which ruptures the veil. The relics of the veil remain as a fringe, the *annulus*, around the stipe (Fig. 69, F).

When fully grown the sporophore is about 4 inches high and the pileus about 5 inches in diameter. The gills appear as radiating plates below the pileus, being pink when young but dark brown later, owing to the ripening of the spores.

The structure of the gill may be seen in a longitudinal section of the pileus (Fig. 69, H). The gill is formed of interwoven hyphæ

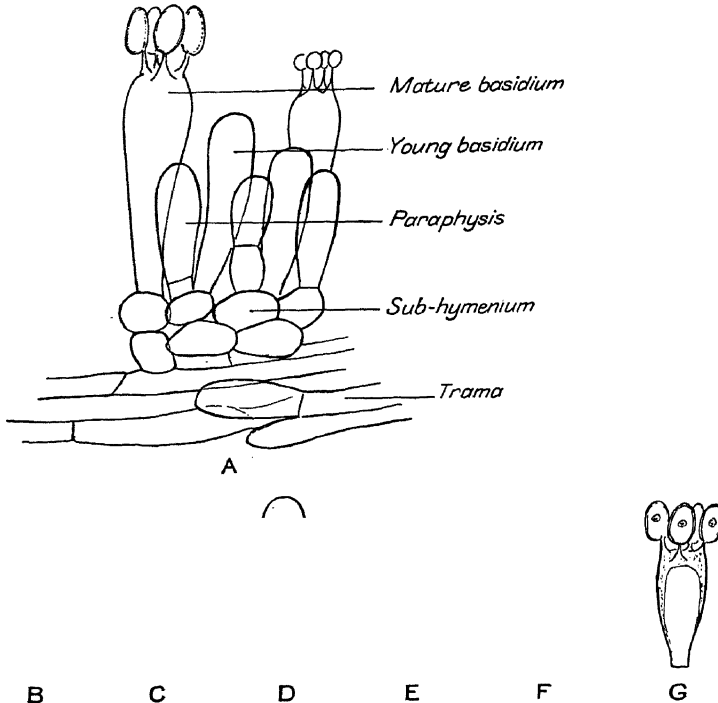


FIG. 70.

A, portion of gill of Mushroom (*Psalliota campestris*) showing development of basidiospores; B, development of basidiospores in *Coprinus* (description in text).

which consist of an inner longitudinal series, the **trama**, a zone of small rounded cells, the **sub-hymenium**, and an outer fringe of elongated cells, the **hymenium**, which produces the spores. The hymenium consists of club-shaped cells of two kinds (Fig. 70, A), viz. **paraphyses**, or sterile cells, and **basidia**, or spore-forming cells.

The process of spore-formation is not yet elucidated in *Psalliota*, but it is probably like that of a closely related toadstool, *Coprinus*, which takes place as follows. The basidium is a binucleate cell

(Fig. 70, B) which commences to form four outgrowths at its free end. The nuclei of the basidium fuse, and the resulting nucleus divides twice to form four (Fig. 70, D). Each outgrowth, or *sterigma*, has, by this time, elongated, and become swollen at the tip to form the main part of a spore (Fig. 70, F). The four nuclei in the basidium squeeze through the sterigmata to pass into the spores at their tips. The mature basidium thus bears four uninucleate spores (Fig. 70, G) which are discharged, when ripe, in a peculiar manner. Buller has shown that, before discharge, a small drop of water is excreted by the sterigma below each spore, and on attaining a certain size, the spore is shot off violently for a distance of about 0.1 millimetre, which is sufficient to project it half-way between two adjacent gills. Arriving here, the spores fall vertically from the pileus, and can be drifted away by air currents. The fact that the gills are usually set in a vertical plane, assists this method of spore-dispersal. The number of spores formed by a single sporophore of *Psalliota* is enormous, an average-sized fructification producing some two thousand million spores.

The spore number for each basidium varies in *Psalliota campestris*, cultivated forms having two, as a rule, whilst wild forms may have the normal four characteristic of the group, or sometimes more. The germination of the spore takes place under suitable moisture and temperature conditions, but takes several weeks to commence.

The commonly cultivated form of the mushroom is a variety, *Psalliota campestris hortensis*. It is propagated artificially by using pieces of the established mycelium, or by culturing hyphæ of the loose central part of the stipe. 'Virgin spawn' may be collected from the mycelia of natural habitats. The hyphæ are grown in moist bricks of dung and soil, which, when permeated with the mycelium, are allowed to dry partially, and form '*mushroom spawn*' used for the inoculation of new mushroom beds.

The family Agaricaceæ includes other edible fungi besides the mushroom, but also includes species which are exceedingly poisonous. *Amanita phalloides*, the Death Cup, is a frequent cause of food-poisoning as it bears some superficial resemblance to the mushroom. It can be distinguished by its white gills and spores, and the swollen sheath, or volva, at the base of the stipe, which is never present in *Psalliota*.

In concluding the description of the Thallophyta, reference must be made to an interesting group of organisms, the Lichens. A lichen is not a single plant, but consists of an alga and a fungus in such close association that they appear to form one individual. This is described as a condition of symbiosis, as it is generally thought that the Alga and the fungus derive benefit from their inti-

mate position. It would seem that the fungus provides satisfactory water conditions for the alga and absorbs nutriment from the poor soils which lichens inhabit, whilst the alga carries out photosynthesis and permits the fungus to use some of the surplus food manufactured. Lichens grow in exposed places, such as bare soil and rock surfaces, and are often the pioneers which prepare such soils for other successors.

Certain lichens are of economic importance, litmus being obtained from species of *Roccella*, and Iceland moss is the thallus of *Cetraria islandica*.

CHAPTER XIV

PTERIDOPHYTA. THE MALE FERN. *SELAGINELLA*

The Pteridophyta are Cryptogams with a much more highly organised structure than has been met with in the members of this sub-kingdom previously dealt with. They are comparable in structure to the Angiosperms, in that they have true roots, stems and leaves, and possess vascular tissues. For this latter reason they are sometimes called the *Vascular Cryptogams*.

The higher organisation of the Pteridophyta is associated with the acquisition of a terrestrial habit which necessitated the development of anchoring absorptive roots and an aerial system bearing photosynthetic structures, the leaves. The internal vascular system was developed to connect the absorbing region of the plant with those parts which could no longer absorb because of the presence of a cutinised epidermis protecting the parts exposed to the atmosphere from desiccation.

The group was probably evolved from simpler ancestors of algal nature, as is indicated by the fact that sexual reproduction involves the formation of motile spermatozoids which require water to effect fertilisation.

The life-cycle of all Pteridophytes embraces two distinct phases, an asexual phase, or *sporophyte*, followed by a sexual phase, or *gametophyte*. This phenomenon is called an *alternation of generations*, and is not confined to the Pteridophyta. It occurs as a regular feature in all groups of plants except the Thallophyta, and does, in fact, occur in some members of that group.

The alternation of generations is connected with sexual reproduction which is invariably brought about by the union of two distinct cells, the gametes.

It was previously stated, in Chapter V, that the chromosome number of the nucleus of the vegetative cell is constant for a particular species. It must be obvious, however, that, even were this the case for every other point in the life-cycle, fertilisation must cause a doubling of the number, as two nuclei fuse. It is found in those plants with an alternation of generations that the gametophyte phase produces gametes which form a zygote from which the sporophyte phase commences. The sporophyte, in due course,

forms spores, asexually, which on germination give rise to gametophytes, and the cycle is repeated.

Asexual spore-formation is accomplished by a special type of nuclear division. This is called the **reduction division**, or **meiosis** (Fig. 73), during which the chromosome number of the original cell becomes halved in the spores. As the spores form gametophytes, the nuclei of these will likewise possess the halved number of chromosomes, as will, also, the gametes. The restoration of the original chromosome number takes place on fertilisation, and the zygote forms a sporophyte whose cells possess this full number. The full chromosome number is called the **diploid number**, usually represented as $2x$, and the halved number is the **haploid number**, represented as x .

It may be noted that the existence of an alternation of generations can be decided, in any plant, on the nuclear history during the life-cycle. The haploid nuclei, formed in the reduction division, are the commencement of the gametophyte phase, which will extend to the point where fertilisation restores the diploid nucleus, which starts the sporophyte phase, continuing until the next reduction.

The two phases of the life-cycle may differ considerably in structure and appearance. In the Pteridophyta, the sporophyte is the obvious plant, which is vascular and generally perennial, whilst the gametophyte is a minute structure, undifferentiated and of temporary duration. In the Bryophyta, the plant division intermediate between the Thallophyta and Pteridophyta, the gametophyte is the dominant phase, but of simple structure, and the sporophyte is a subsidiary structure which is attached, throughout its development, to the gametophyte.

In several Algæ, the gametophyte and sporophyte are morphologically identical, and only on the production of reproductive bodies are they readily distinguished.

The Pteridophyta consist of the Filicales, or Ferns, the Equisetales, or Horsetails, and the Lycopodiales, or Clubmosses, these groups differing in their vegetative structure and their methods of spore-production.

The Ferns are the only terrestrial Cryptogams which can compete successfully with the higher plants.

The Male Fern (*Dryopteris Filix-mas* ¹)

The Male Fern is a common British fern, growing abundantly as a herbaceous perennial in shady woods and hedgebanks, and occasionally in more exposed situations such as hillsides. The obvious

¹ At various times, this plant has been referred to the genera, *Lastræa*, *Aspidium* and *Nephrodium*.

plant is the sporophyte, which, when fully developed, consists of a short oblique rhizome clothed with the bases of leaves of former years (Fig. 71, A), and bearing, during the spring and summer, a crown of large compound leaves, or *fronds*.

The apex of the rhizome appears to be occupied by a compact terminal bud, but this is formed by a number of young leaves which have arisen singly. The young leaves are covered with brown chaffy scales, or *ramenta*, which serve to protect them against water-loss and are gradually shed as the leaf unfolds. The leaf unfolds in the spring by the elongation of the lower part which raises the younger apex, still coiled in a crozier-like form. This *circinate vernation* is a character of ferns in general. The root system consists of a large number of tough adventitious roots which arise from the leaf-bases.

The mature leaf consists of a stalk, the *stipe*, which continues as the mid-rib, or *rachis*, of the compound lamina, which is composed of a number of pairs of leaflets, or *pinnæ*, further subdivided into *pinnules*. The leaf is typically dorsiventral, and may be solely vegetative, or may bear the spore-producing structures, or sporangia, in which case it is called a *sporophyll*. The internal structure of the sporophyte is very similar to that of the seed-plants. The rhizome elongates by apical growth, its tip being occupied by a tetrahedral *initial cell*, which has its apex directed inwards, and its broad base outwards. From the three inner sides of the initial cell segments are cut off in regular sequence, and by further division of these a multicellular tissue is produced. There is no similarity here to the behaviour of the apex of the Angiosperm stem, with its three meristematic histogens, which produce a stratified appearance from the outset. In the fern rhizome, the outermost or superficial cells differentiate to form the epidermis, and the inner cells give rise to the ground parenchyma and the vascular tissues, as the apex extends.

The leaves arise immediately behind the stem-apex, from superficial cells which divide to form two-sided apical cells. By the continued division of these cells, the dorsiventral symmetry of the leaves is produced. The apex of the root is occupied by a tetrahedral initial cell, similar to that of the rhizome. This cell cuts off segments to the inside like that of the rhizome, but, in addition, cuts off segments to the outside by walls parallel to the outer surface, to form a root-cap, which is replaced from within like that of the Angiosperms.

A transverse section of the rhizome (Fig. 71, B), shows a series of vascular strands arranged in a ring in a parenchymatous ground tissue rich in starch. The structure of the stele is not appreciated

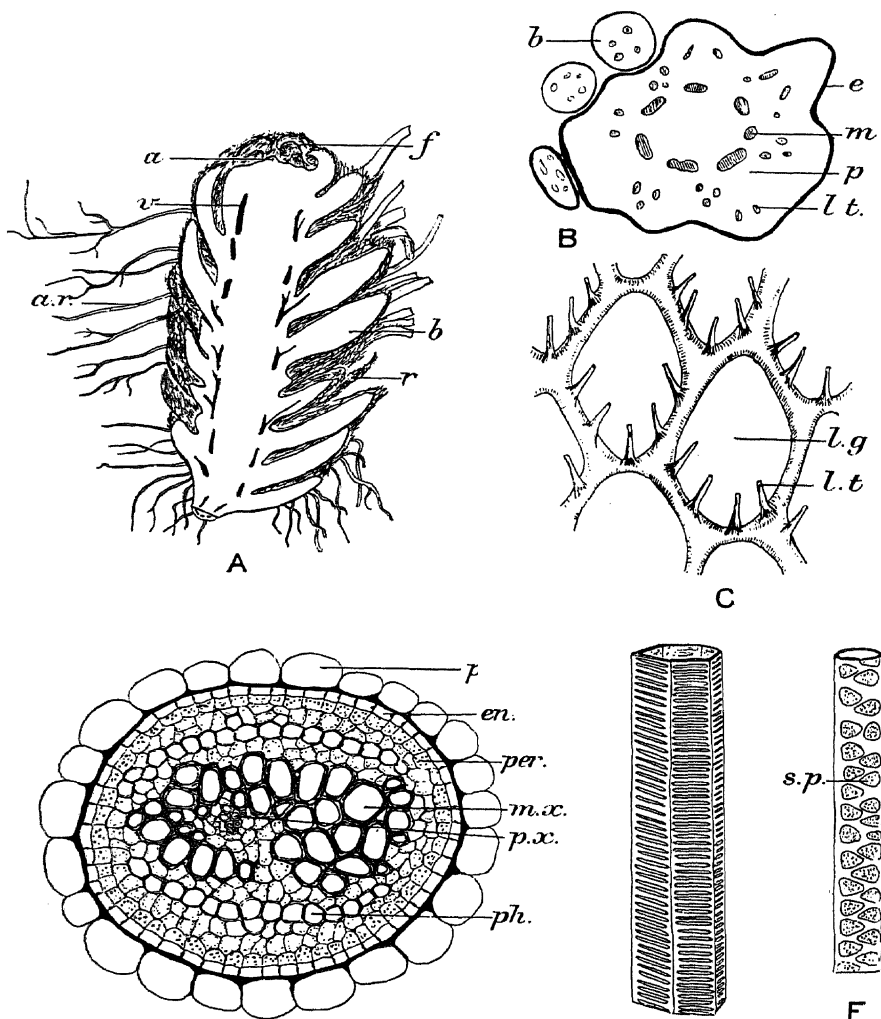


FIG. 71.—Male Fern (*Dryopteris Filix mas*).

A, longitudinal section of rhizome ($\times \frac{1}{2}$); B, transverse section of rhizome ($\times 2$); C, part of dictyostele (enlarged); D, transverse section of meristele in detail; E, part of scalariform tracheid of metaxylem; F, part of sieve-tube.

(a = apex of rhizome, a.r. = adventitious root, b = base of frond, e = epidermis, en. = endodermis, f = young frond, l.g. = leaf-gap, l.t. = leaf-trace, m = meristele, m.x. = metaxylem, p = ground parenchyma, per. = pericycle, ph. = phloem, p.x. = protoxylem, r = ramentum, s.p. = sieve-plate, v = vascular system.)

THE MALE FERN

from a transverse section only, for when it is dissected on entirety (as may be done by treatment of the rhizome with acid and carefully brushing away the softened tissues) it is seen to be a reticulate, or net-like, cylinder. This type of stele is called a *dictyostele* (Fig. 71, c), and the gaps in the mesh indicate the points at which leaves arose, the vascular strands, or leaf-traces, of the leaves being given off from the lower strands of the *leaf-gaps*. Returning to the transverse section, it will now be realised that each strand, appearing like an ordinary vascular bundle, is part of a more elaborate system, and is called a *meristele*. The meristele (Fig. 71, d) consists of a central xylem, surrounded by phloem, the whole being bounded by pericycle and endodermis. Because of the positions of xylem and phloem the meristele is *concentric* and *amphicribal*.

The endodermis forms a continuous layer, without intercellular spaces, and the walls of the ground tissue outside it are thickened. The pericycle is ill-defined and arises from the same mother-cells as produced the adjacent endodermal cells. The phloem consists mainly of large thin-walled sieve-tubes which are elongated cells with tapering ends and cellulose walls. Where two sieve-tubes adjoin, numerous small sieve-areas occur (Fig. 71, f). The sieve-tubes are not accompanied by companion cells.

The phloem is separated from the xylem by small parenchymatous cells which are not readily referred to either xylem or phloem, and is called the *conjunctive parenchyma*.

The chief feature of the xylem is the large metaxylem elements. These are tracheids with oblique ends and having transverse slit-like pits, which produce the typical scalariform appearance (Fig. 71, e), found in the xylem of all members of the Pteridophyta. Embedded in the metaxylem, amongst a small amount of parenchyma, are one or more groups of protoxylem tracheids which are spirally or reticulately thickened. Because the protoxylem is surrounded by metaxylem it is said to be *mesarch*.

The transverse section of the root in the absorbing region shows an outer piliferous layer with root-hairs, a comparatively wide cortex and a central stele. The inner cortex usually consists of cells with lignified walls, which strengthen the root. The stele has an outer pericycle, generally several cells deep, a central diarch xylem with protoxylem at each end, and two phloem groups, one on either side the xylem.

The structure of the leaf is similar to that of the dorsiventral leaf of shade-loving Angiosperms. There is a single-layered epidermis, usually containing chloroplasts, and penetrated on the lower side by typical stomata. The mesophyll is differentiated into an upper

shallow palisade tissue, and a lower spongy tissue with numerous intercellular spaces. The vascular bundles of the main veins are collateral, with the xylem uppermost, and are surrounded by lignified bundle-sheaths.

The Male Fern sporophyte resembles a herbaceous Angiosperm in that all growth is primary, and the nutrition is autotrophic.

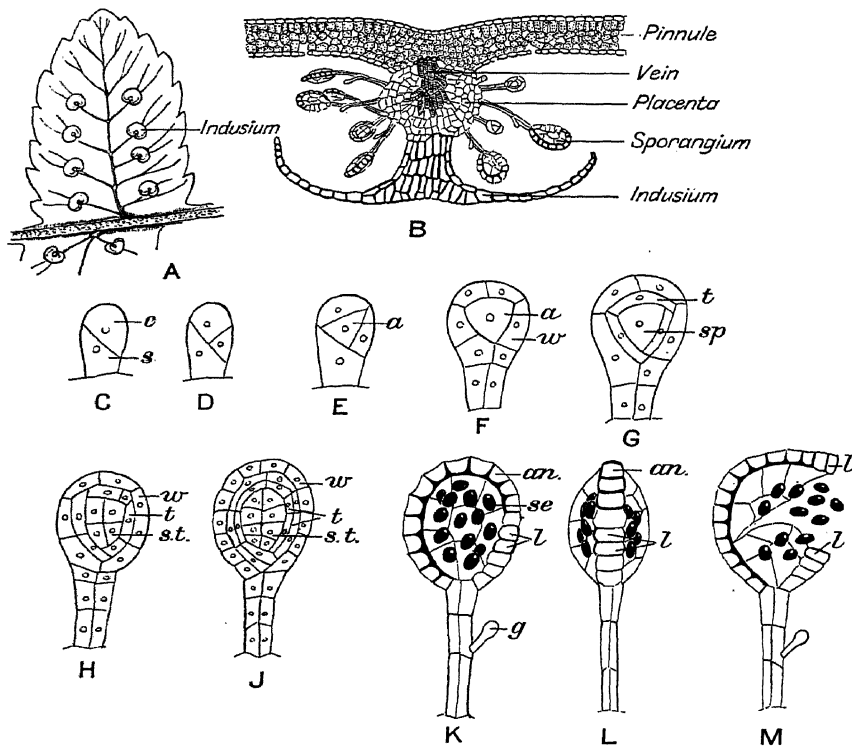


FIG. 72.—Male Fern.

A, dorsal surface of pinnule ($\times 4$); B, transverse section of pinnule, through sori; C–M, development of sporangium (description in text). (α = archesporium, $an.$ = annulus, c = capsule-cell, g = glandular hair, l = lip-cells of stomium, s = stalk-cell, $se.$ = spore, $sp.$ = sporogenous cell, $s.t.$ = sporogenous tissue, t = tapetum, w = wall.)

During the summer spore-production occurs. The sporophylls differ little from ordinary vegetative leaves which are the only type formed when the plant is young.

The sporangia are formed on the backs of the pinnules in groups, or *sori*, each covered by a kidney-shaped scale, the *indusium* (Fig. 72, A). The sori are produced below certain veins and form a double row along the pinnule.

The sorus commences as a parenchymatous swelling, or *placenta*, the central part of which grows downwards and outwards to form the indusium, which protects the sporangia developing on the rest of the placenta.

A transverse section of the pinnule (Fig. 72, B) shows the general arrangement in the sorus. The mature sporangium (Fig. 72, K) is attached to the placenta by a thin multicellular stalk (often bearing a glandular hair), which terminates as a swollen, biconvex *capsule* containing spores. A median crest of thickened cells, the *annulus*, runs along one edge of the capsule to half-way along the other side, where the wall consists of thin-walled cells marking the point of dehiscence of the capsule. In the Male Fern the capsule contains forty-eight spores, but in most ferns the capsule contains sixty-four.

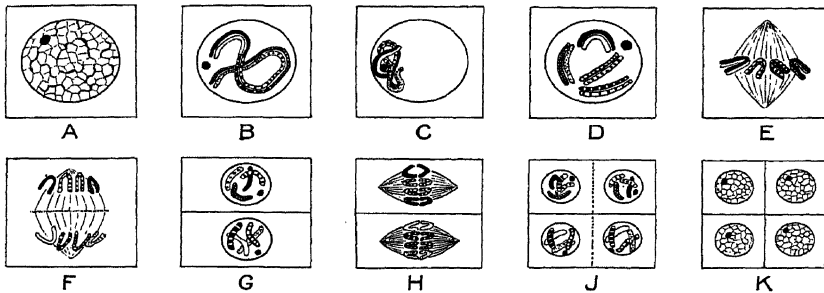


FIG. 73.—Diagram of stages in the reduction division (meiosis) of a spore-mother-cell.

In order to show the behaviour of individual chromosomes, each is marked in the same manner throughout. For description see text.

Each sporangium arises as a surface cell of the placenta. This cell divides to form a lower stalk-cell, and an upper capsule-cell (Fig. 72, o). By further division of the capsule-cell, a central cell bounded by a single-layered wall is formed (Fig. 72, r). Division of the central cell gives rise to an inner sporogenous tissue surrounded by a double layer of nutritive cells, the *tapetum* (Fig. 72, H). The sporogenous tissue ultimately consists of twelve *spore-mother-cells*, each of which forms four spores by a reduction division in the following manner. The chromatin of the nucleus becomes more prominent and contracts to one side of the nucleus; this is a condition called *synapsis* (Fig. 73, c). It then becomes more dispersed and breaks up into a number of chromosomes which are associated in longitudinal pairs (Fig. 73, D). This results in an apparent halving of the chromosome number, for whereas the original nucleus of the spore-mother-cell of the Male Fern had one

hundred and twenty-eight chromosomes, at this stage there are sixty-four double-chromosomes. It is thought that the pairing of chromosomes in the reduction division represents an association of chromosomes derived respectively from the male and female gametes of the previous fertilisation.

Subsequent events resemble closely those of ordinary mitosis, for they include the disappearance of the nucleolus and the nuclear membrane and the formation of the nuclear spindle, at the equator of which the double-chromosomes are arranged (Fig. 73, *н*). Further, the double-chromosomes behave like the individual chromosomes of mitosis, in that their component chromosomes separate and pass to the opposite poles of the spindle, in what is known as the *heterotype* division (Fig. 73, *р*). In this way a group of chromosomes, each consisting of half the number of the original spore-mother-cell occurs at each pole, and forms a daughter-nucleus. The two daughter-nuclei, thus formed, immediately undergo a second, or *homotype* division (Fig. 73, *н*), which is identical with mitosis and results in the formation of a group of four cells, or a *tetrad*, each with the reduced, or haploid, number of chromosomes (Fig. 73, *ж*, *к*). These cells enlarge slightly, separate and become rounded to form the asexual spores, which, when ripe, have a two-layered coat.

The ripe spores are shed from the sporangia under dry conditions, when they may be widely scattered in the air. As the sporangium matures the wall-cells gradually dry, and the annulus, because of its peculiar thickening, shrinks and sets up a tension which is suddenly released by the rupture of the wall at the thinner part, or *stomium*. The annulus springs back and tears, with it, the upper half of the capsule, so releasing the spores (Fig. 72, *м*), which may be thrown out more effectively by the quick recovery of the annulus to its original position.

Although the fern spore is essentially a structure developed for dispersal under dry conditions it will not undergo further development unless supplied with moisture, and a suitable temperature. The spore is the first cell of the gametophyte generation, as it possesses a haploid nucleus. On germination, the outer layer of the spore-coat is broken and the spore-contents enlarge and push out the inner thin coat, which therefore becomes the cell-wall.

By division of the spore, a short filament of cells is produced, some of the cells containing chloroplasts and others becoming elongated and colourless to form anchoring cells, or *rhizoids* (Fig. 74, *в*). After a time, a small flat green *prothallus* has been formed, which is roughly heart-shaped, and is closely attached to the moist soil by numerous unicellular rhizoids on its lower surface,

near the pointed end (Fig. 74, D). The prothallus contrasts greatly with the sporophyte, for it shows little differentiation and resembles a thalloid Alga. It is one cell thick, except for a central parenchymatous zone, the *cushion*, and with the exception of the rhizoids, all the cells contain numerous chloroplasts. There is no conducting tissue, but as the cell-walls are uncutinised, water can be absorbed at any point over the surface of the prothallus. The absence of cuticle, or other similar protection, means that the prothallus must complete its development under conditions of abundant moisture, for even a short period of desiccation would result in death. The dependence of the prothallus on water is even more emphasised during sexual reproduction, which is brought about through its agency.

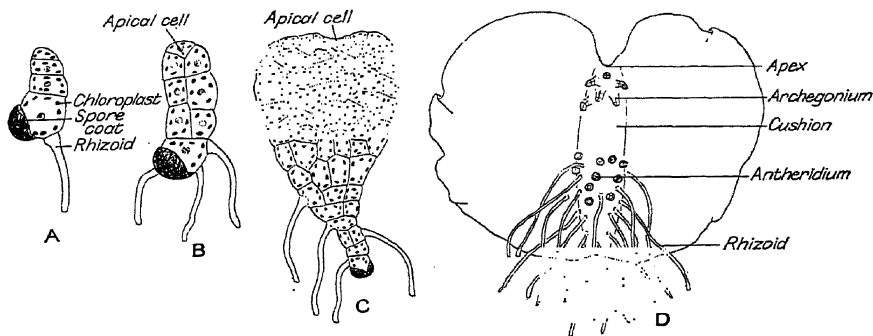


FIG. 74.—Male Fern: development of prothallus (all stages much enlarged); D, view of lower surface of mature prothallus.

Male and female organs are usually formed on the same prothallus, being borne on the cushion on the lower surface, in contact with moisture.

Antheridia arise first, and are situated towards the pointed end of the prothallus, often amongst the rhizoids. Each is formed from a single cell which divides to produce a three-celled wall enclosing a central group of cells, the *spermatocytes* (Fig. 75, H). The female organs, known as *archegonia*, arise on the cushion, nearer to the broad end of the prothallus. As in the case of the antheridium, each archegonium commences as a single cell, which divides to form a *venter*, sunk in the cushion, and a short projecting *neck* (Fig. 75, A–C). When mature the archegonium consists of a central row of cells surrounded by a wall of cells. The lowermost central cell, situated in the venter, is the single female gamete, or egg-cell, above which are a small *ventral-canal-cell*, and a longer *neck-*

canal cell occupying the centre of the neck. The neck consists of four longitudinal rows of cells enclosing the neck-canal-cell. When the egg-cell is ready for fertilisation, the neck curves slightly; towards the position of the antheridia, the neck-canal-cell becomes disorganised and mucilaginous, and forces open the top of the neck, making access to the egg-cell possible (Fig. 75, D). About this time

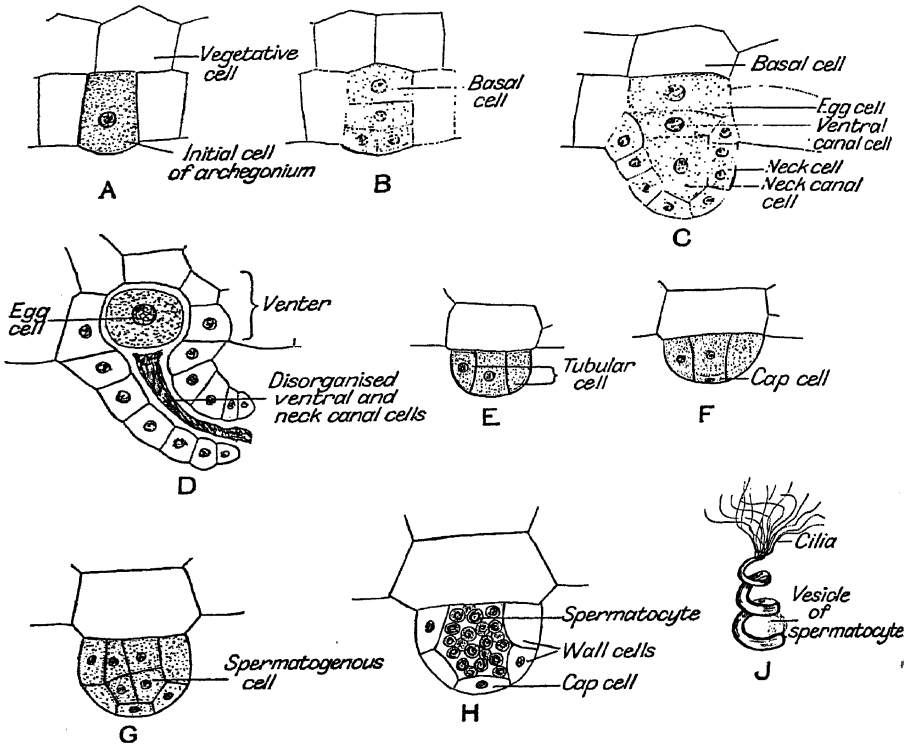


FIG. 75.—Male Fern.

A–D, stages in development of archegonium; E–H, stages in development of antheridium; J, spermatozoid, highly magnified.

the antheridia have ripened and liberated the male gametes, each spermatocyte having formed a spermatozoid with a spirally coiled body and a terminal tuft of cilia (Fig. 75, J).

In order to reach the archegonia, the spermatozoids require water which is provided by the thin film present on the soil surface below the prothallus. Fern spermatozoids afford an example of

positive chemotaxis, as they are attracted to the archegonium by the mucilage containing malic acid secreted by the open neck canal.

Several spermatozoids may enter the neck of the archegonium, but one, only, proceeds to the egg-cell which it enters and effects fertilisation.

The resulting zygote, the initial cell of the sporophyte phase, commences to divide in the venter to form an embryo. Only one embryo is formed by the prothallus, although many archegonia are produced.

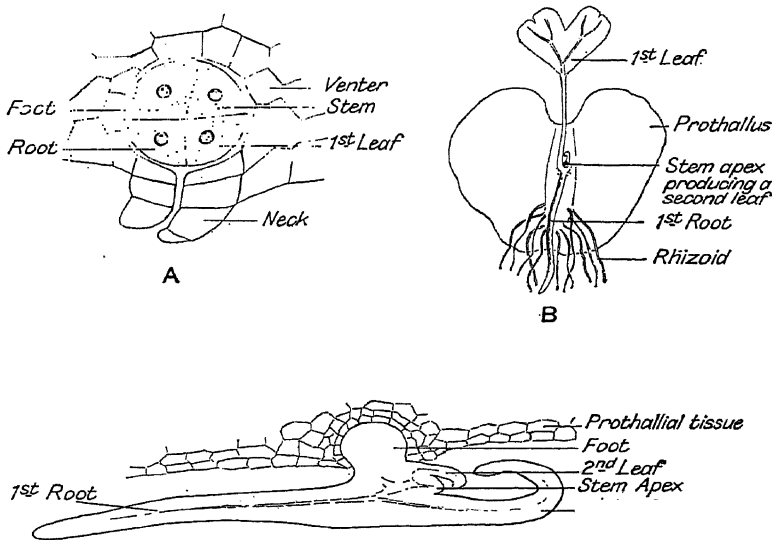


FIG. 76.—Male Fern.

A, longitudinal section through young embryo, in venter of archegonium; B, prothallus with young sporophyte (enlarged); C, longitudinal section through young sporophyte attached to prothallus.

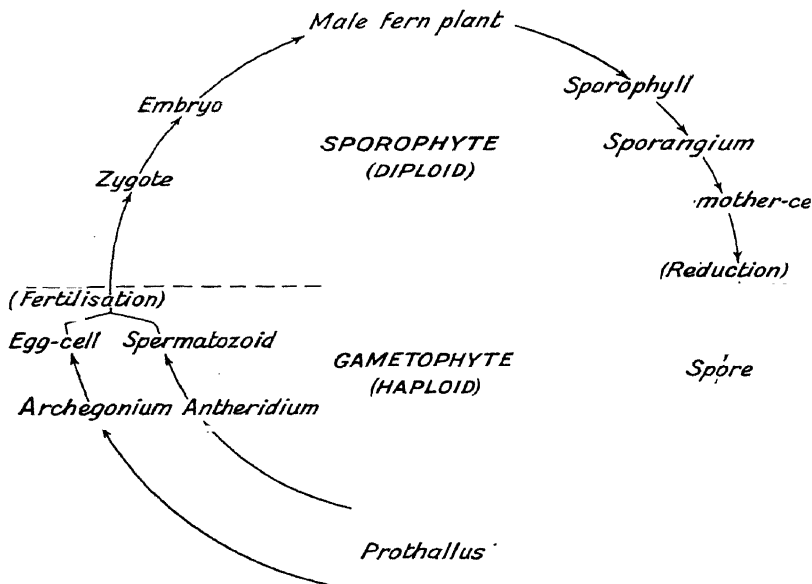
The early division of the zygote results in a globular embryo composed of four zones which become respectively, an absorptive **foot**, stem apex, primary root and first frond, of the young sporophyte (Fig. 76, A).

The foot is a suctorial organ, closely applied to the prothallial tissue, from which it obtains the food needed by the young sporophyte, before the sporophyte is capable of obtaining it for itself. The sporophyte, at this stage, is parasitic on the prothallus. By further growth of the embryo, the primary root and frond emerge from the lower side of the prothallus (Fig. 76, B, c). The root enters

the soil and the frond expands, establishing the sporophyte as an independent plant, after which the prothallus dies and decays.

Several years are required for the new sporophyte to reach maturity, but this depends on environmental conditions, including the proximity of competing plants.

The life cycle is summarised below :



Selaginella (Fig. 77)

Selaginella is a genus of the Lycopodiales, which includes a large number of species occurring, for the most part, in warmer regions of the world, although a single species is found as a rare plant in Britain.

Selaginella Martensii is frequently grown in greenhouses, and may easily be obtained for purposes of study.

The obvious plant is the sporophyte which consists of a branched shoot system composed of slender stems bearing small sessile leaves closely applied to them.

The reproductive shoots take the form of loose cones, or **strobili**, borne apically by certain branches. Each strobilus consists of a central axis bearing whorls of scale-like sporophylls (Fig. 77, A). The sporophyll bears a single sporangium at the bottom of its upper surface and two types of sporangia are found in each strobilus.

Certain sporophylls, the **microsporophylls**, bear globular sporangia containing numerous minute **microspores**, whilst others, the **megasporophylls**, bear lobed sporangia, each containing four large **megaspores**. As *Selaginella* produces two kinds of asexual spore it is said to be **heterosporous**, in contrast to such plants as the Male fern, which is **homosporous**, as it produces one kind of spore only. The occurrence of the heterosporous habit in the

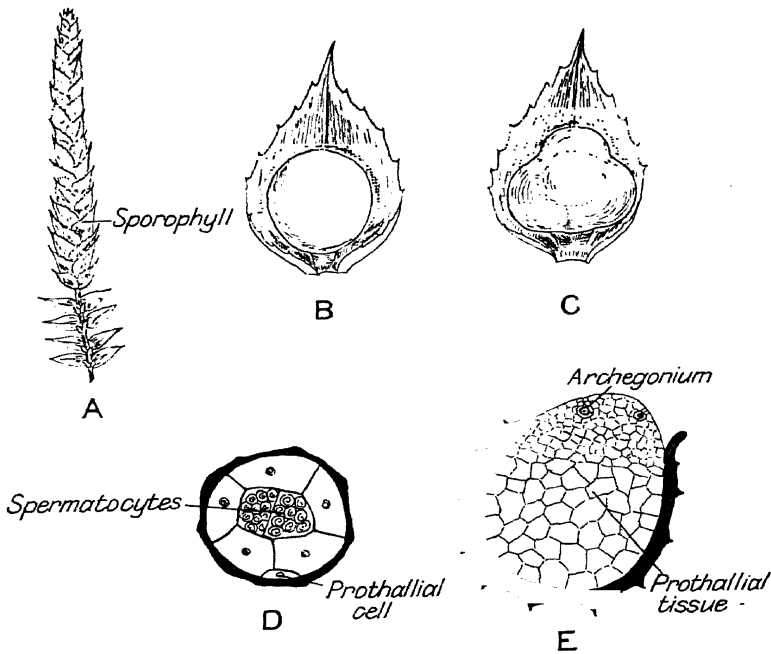


FIG. 77.—*Selaginella Martensii*.

A, cone; B, upper surface of microsporophyll with microsporangium; C, upper surface of megasporophyll with megasporangium; D, microprothallus within microspore-coat; E, megaprothallus, surrounded by megaspore-coat.

Pteridophyta is of great interest as it is a feature of all the members of the Spermatophyta.

On germination, the two kinds of spore of *Selaginella* form different types of gametophyte. The microspore forms a male prothallus, and the megaspore a female prothallus.

The development of the microspore takes place whilst it is still enclosed in the sporangium, and consists in a number of cell-divisions without enlargement, so that the spore-coat is not ruptured. A single vegetative, or **prothallial cell** is formed, and the rest of the

microprothallus represents an antheridium consisting of two central cells surrounded by a wall of cells. The central cells divide to form four or more spermatocytes, which later become biciliate spermatozoids.

The megaspore also commences its development within the sporangium, but in *Selaginella Martensii* it is then shed to complete the formation of the *megaprothallus*. By repeated division, a multinucleate mass is formed followed by cell-wall formation to produce a multicellular prothallus. A number of simple archegonia arise near the surface of one side of the prothallus, each consisting of a venter and neck both submerged in prothallial tissue. Prior to fertilisation, the megaprothallus swells to burst the spore-coat at the point where the archegonia occur, so exposing the archegonia on a slight protrusion.

Both the megaprothallus and the microprothallus are non-green and have developed entirely at the expense of food present in the original spores.

Fertilisation requires the presence of water, in which the liberated spermatozoids can swim to the archegonia of megaprothalli in their vicinity.

The zygote formed on fertilisation commences development immediately, cutting off a small cell, or *suspensor*, an absorptive foot, and a stem apex, which produces leaves and an adventitious root at a later stage.

In due course the sporophyte becomes an independent plant and the cycle continues.

An interesting variation is found in *Selaginella rupestris*, the megasporangium of which may contain fewer than four spores. In this plant the megaprothallus develops completely whilst the structure is in the megasporangium. The microspores are shed amongst the megasporophylls, where they germinate. On the opening of the megasporangium, fertilisation can take place, whilst the megaprothallus still occupies it, and the early stages of the embryo are developed in the same position.

These events approach those which take place in the seed-plants, and serve to illustrate the similarity of the life-history of the members of the two divisions of vascular plants, viz. Pteridophyta and Spermatophyta.

In *Selaginella rupestris*, the young sporophyte, together with the remains of the megaprothallus which has been nourishing it, eventually falls from the parent-sporophyte and becomes established as an independent plant.

CHAPTER XV

SPERMATOPHYTA, 1. GYMNOSPERMÆ. *PINUS SYLVESTRIS*

The Spermatophyta or Seed-plants form the dominant vegetation of the world, at the present time, both from the points of view of size and numbers. The size, however, shows considerable variation, as has been indicated in considering the general form of plants in Chapter II.

The character of the Spermatophyta, which distinguishes them from other plants, is the production of a complex reproductive body, the seed, which results from a fertilisation, involving a structure called a *pollen-tube*. The formation of a pollen-tube, which will be seen later, to represent the male gametophyte, enables male gametes to be carried directly to the female without the necessity of water.

The method of sexual reproduction makes the Seed-plant less dependent on water than some of the earlier groups of plants, but other features also have been developed, which explain the great success of the Spermatophyta as land plants. The seed, with its thick testa, and resistant protoplasm, can undergo desiccation without losing its viability. The vegetative organs are specialised for a terrestrial habit, and include an efficient root system, well-developed vascular tissues, and protective dermal systems (either cutinised or suberised), all of which enable the plant to be exposed to the drying atmosphere without harm. It is true that some Seed-plants live in water. These aquatics are regarded as descendants of terrestrial plants, which have become specialised for their mode of life, and escaped from the greater competition between species, experienced on land. Aquatic Seed-plants are, for the most part, dependent on aerial flowers for reproduction.

The ancestry of the Spermatophyta is problematic, and there is evidence, from the fossil record, that they were in existence many thousands of years ago. A certain fossil plant, now entirely extinct, was *Lyginopteris*, which flourished as a climber in the geological period called the Coal Measures. *Lyginopteris* had a vegetative structure not unlike that of some of the modern ferns, but it repro-

duced itself by true seeds. From a study of this and similar forms, it was once thought that the seed-plants descended directly from Pteridophyte ancestors, although these were not necessarily identical with existing types. Some fossil Pteridophytes had woody stems with secondary growth, like that of the present Gymnosperms and Dicotyledons.

The probability is that the Spermatophyta and the Pteridophyta had a common ancestry, but at present it is pure hypothesis as regards the appearance of the ancestral form. It will be seen from a comparison of the existing members of the two groups that there are certain close resemblances, but also well-marked differences.

The Spermatophyta consists of two sub-divisions, the Gymnospermæ and the Angiospermæ, which are distinguished by their methods of seed-production and other characters.

The Gymnosperms bear openly exposed seeds on their carpels, whereas in the Angiosperms the carpel encloses the seeds completely as the fruit is formed.

There are several classes of Gymnosperms, but the most important is the Coniferæ which includes the pines, spruce, larch, yew and other well-known trees. This class is of economic importance as various members yield timber (deal), turpentine and resin.

The Scots Pine (*Pinus sylvestris*)

The Scots pine grows naturally in certain parts of Britain, especially in the north, where it is found on somewhat acid sandy soils in open situations.

The tree represents the sporophyte phase of the life-cycle, but is very unlike the sporophyte of the Male fern. It is a woody evergreen, bearing narrow needle-like leaves, and reaches a height of about 50 feet in favourable situations.

The woody trunk elongates, year by year, by the continuation of the apex, and forms whorls of branches, in succession, from the lateral buds of each season. When growing in exposed positions the tree does not maintain the normal monopodial system of growth, owing to the death, by damage, of the leading shoot, and often, also, of the ends of lateral branches. The compensatory growth, by the activity of lateral buds, generally gives the old tree a very irregular appearance. The younger twigs of the main branches are clothed with brown scale-leaves, the bases of which are thick, and closely applied to the stem, giving it a rough surface. From the axils of the scale-leaves *dwarf-shoots* arise (Fig. 78), each consisting of a short stem bearing thin scale leaves and a pair of long thin foliage leaves. The restriction of the foliage leaves to dwarf-shoots, or *fascicles*, is a feature of all species of *Pinus*, although the number

of leaves is not invariably two. The foliage leaf is a xerophytic structure, having a reduced surface, thick cuticle and sunken stomata situated in grooves running along the leaf. In transverse section (Fig. 79) it shows a type of anatomy described as *centric*, the central vascular system, of two bundles, being surrounded by a

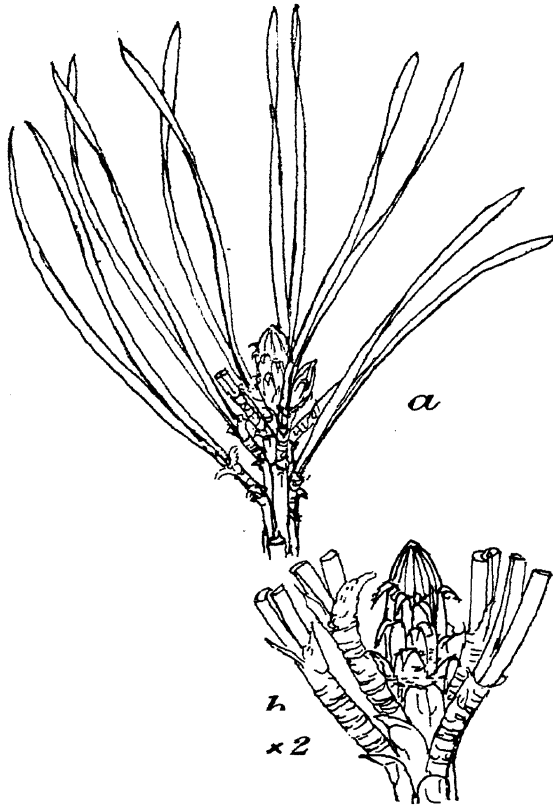


FIG. 78.—Scots Pine (*Pinus sylvestris*).

a. twig terminated by a winter bud and bearing dwarf-shoots ($\times 1$); *b.* apex of twig, showing bases of dwarf-shoots and their arrangement in the axils of scale-leaves of the twig.

parenchymatous *transfusion tissue*, which is enclosed by a compact mesophyll. The mesophyll is composed of cells, fitting closely together, the cell-walls being infolded to increase the area bearing chloroplasts. Large transverse air-spaces occur in the mesophyll, but these can only be seen in a longitudinal section of the leaf. The epidermis bears a thick cuticle, which prevents excessive

water-loss, and beneath the epidermis is a fibrous hypodermis which is an additional protection.

The anatomy of the stem and root (Fig. 80) agrees closely with that of the same organs of a woody Dicotyledon, both with regard

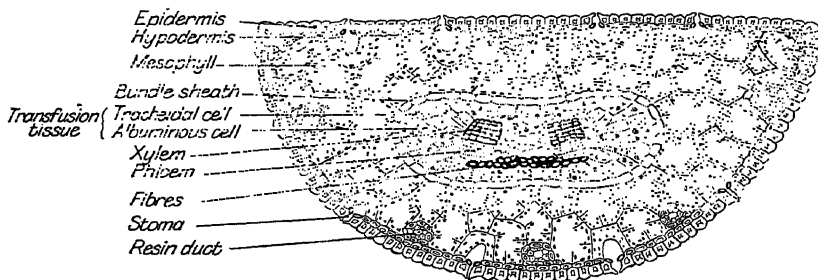


FIG. 79.—Transverse section of leaf of Scots Pine.

to the arrangement of tissues and the type of secondary growth. Secondary growth of the stele is effected by a cambium, and a corky periderm is formed, on the outside of the organs, by the activity of a phellogen.

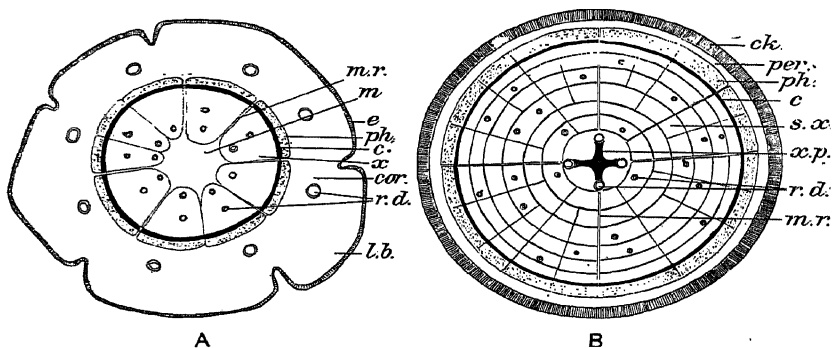


FIG. 80.—Scots Pine (*Pinus sylvestris*).

A, transverse section of one-year-old stem, plan of tissues; B, transverse section of woody root, plan of tissues.

(c = cambium, ck. = cork, cor. = cortex, e = epidermis, l.b. = leaf-base, m = medulla, m.r. = medullary ray, per. = pericycle, ph. = phloem, r.d. = resin duct, s.x. = secondary xylem, x = xylem, x.p. = primary xylem.)

The vascular elements of the pine, however, resemble those of a Pteridophyte rather than those of the Angiosperms, as the xylem is composed of tracheids, and the sieve-tubes of the phloem are unaccompanied by companion cells. The tracheids of the meta-xylem and secondary xylem of all Gymnosperms are distinctive,

as the radial longitudinal walls of each bear a single row of large bordered pits (Figs. 29, 81).

The vascular rays of the woody stem differ in certain respects from the similar structures of the woody Dicotyledon. They are one cell wide, and differ in composition in the phloem and xylem (Fig. 81). The xylem portion of the ray consists of a central row of cells containing starch, and outer cells with pitted lignified walls. The phloem portion possesses the same type of central cells, but the outer cells are elongated and contain nitrogenous contents.

A feature of all organs of the pine are the *resin ducts*. They occur in the pericyclic parenchyma of the young stem, in the protoxylem of the root, in the mesophyll of the leaf, and in small parenchymatous islands in the secondary wood of stem and root.

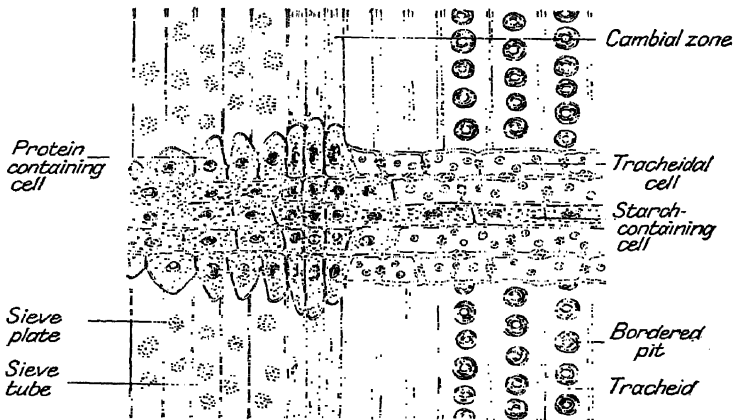


FIG. 81.—Radial longitudinal section through part of vascular tissue of woody stem of *Pinus*, showing a medullary ray.

The resin duct is formed by the division of cells surrounding an intercellular space of the young organ. When fully formed it consists of a circle of secretory cells enclosing a canal, which was the former intercellular space, into which resin is secreted. Such a duct, formed by the enlargement of an intercellular space, is described as *schizogenous*.

Although the Scots pine is evergreen and does not shed its leaves completely each autumn, it exhibits the same seasonality as the deciduous tree. The apices of the shoot are protected inside buds with corky resinous bud-scales and these buds remain dormant during the winter, and develop in the following spring. On opening in the spring each bud gives rise to a new twig bearing the characteristic dwarf-shoots, and in some cases, also, reproductive shoots.

The reproductive shoots take the form of cones, not unlike those of *Selaginella* in composition except that in *Pinus*, microsporophylls and megasporophylls are confined to separate cones. The two kinds of cone differ in appearance and are known as male, or

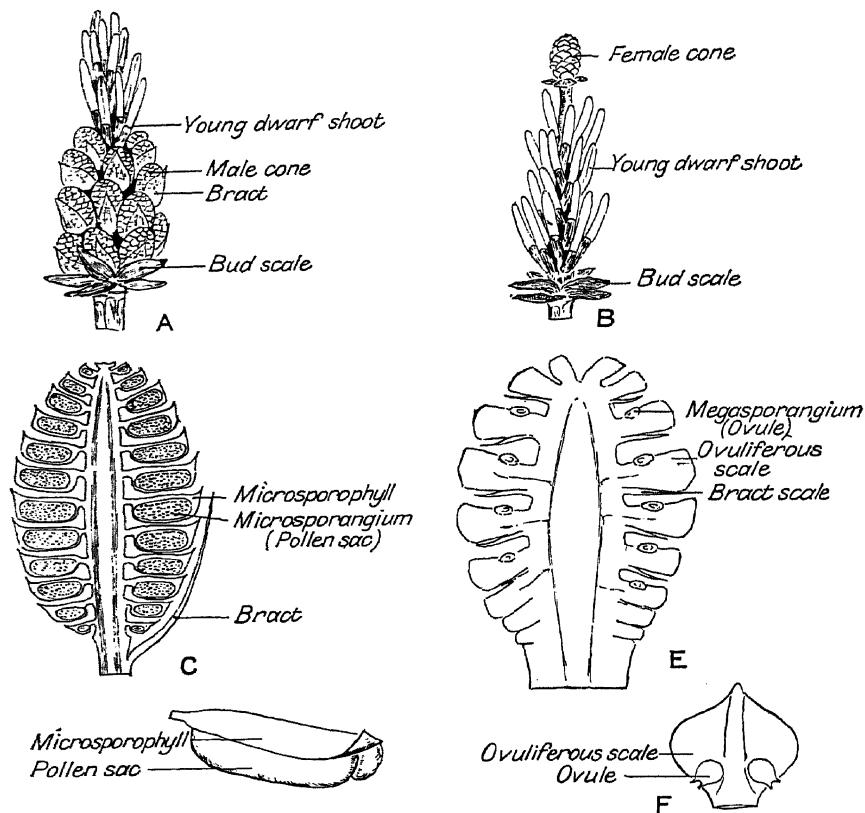


FIG. 82.—Scots Pine (*Pinus sylvestris*).

A, young shoot bearing male cones ($\times 1$); B, young shoot with female cone ($\times 1$); C, longitudinal section through male cone (enlarged); D, single microsporophyll; E, longitudinal section through female cone (enlarged); F, single megasporophyll, upper surface.

staminate, and female, or **carpellate** cones respectively. Both are found on the same tree.

The male cones (Fig. 82, A) arise in the spring, in a cluster at the base of the new twig developed by an opening bud. Each cone is a yellow egg-shaped body about $\frac{1}{4}$ inch long. It is in the axil of a transparent scale-leaf of the twig, and thus occupies a position

similar to the vegetative dwarf-shoots which are forming higher up the twig. The male cone consists of a central axis on which a crowded spiral series of microsporophylls is arranged (Fig. 82, c). The microsporophyll (Fig. 82, d) has a short stalk and an expanded portion, bearing on its lower surface two elongated microsporangia or *pollen-sacs*. The structure of the microsporangium is essentially the same as that of *Selaginella*, containing, in its early stages, microspore-mother-cells (also known, in *Pinus*, as *pollen-mother-cells*) surrounded by a nourishing tapetal layer. Each mother-cell undergoes meiosis to form a tetrad of microspores or *pollen-grains*.

The female cones (Fig. 82, B, E) appear shortly after the male on the upper part of the new season's shoots, frequently on those which also bear male cones. Each female cone is a small red structure, situated immediately below the apex of the twig, in the position normally occupied by lateral buds on purely vegetative shoots. It is slightly longer than the male cone and stands erect on a short stalk. As in the male, a series of sporophylls (in this case megasporophylls) is arranged spirally on a central axis. The megasporophyll is a fleshy scale bearing two megasporangia or *ovules*, and it is situated immediately above a thin scale, known as the *bract scale*, to distinguish it from the megasporophyll, which is also known as the *ovuliferous scale*.

The development of the megasporangium, or ovule, is not so obvious as that of the microsporangium, and it is largely the nuclear behaviour of the contents which affords the clue to its true nature. The ovule arises near the base of the upper surface of the megasporophyll as a small parenchymatous swelling, the *nucellus* (Fig. 83, A). From the base of the nucellus a collar-like investment is formed which grows round the nucellus, as the *integument*, to enclose it completely, except for a small pore, or *micropyle*, at the inner end (Fig. 83, B). A cell with dense contents and a prominent nucleus appears in the nucellus; this is the megaspore-mother-cell (Fig. 83, B), which undergoes a reduction division to form a row of four haploid cells which represent megaspores (Fig. 83, D). Of the four megaspores, three degenerate, and a single large one survives in the nucellar tissue. The further divisions of this solitary megaspore will represent the female gametophyte.

The gametophytes of *Pinus* are inconspicuous, for they have undergone even more reduction than those of *Selaginella*, and the female gametophyte is never liberated from the megasporangium.

The original microspore is a uninucleate cell (Fig. 84, A), which commences to form a microprothallus whilst contained in the pollen-sac. The simple male gametophyte is produced within the

two-layered spore-coat, by a number of nuclear divisions, unaccompanied by enlargement. The microprothallus consists of two flattened *prothallial cells*, a *generative cell* with nucleus surrounded by cytoplasm, and a *tube nucleus* occupying the cytoplasm of the main portion of the original spore (Fig. 84, D). The prothallus, or pollen-grain, is shed in this condition, but before dispersal, two air-sacs are formed as local swellings between the

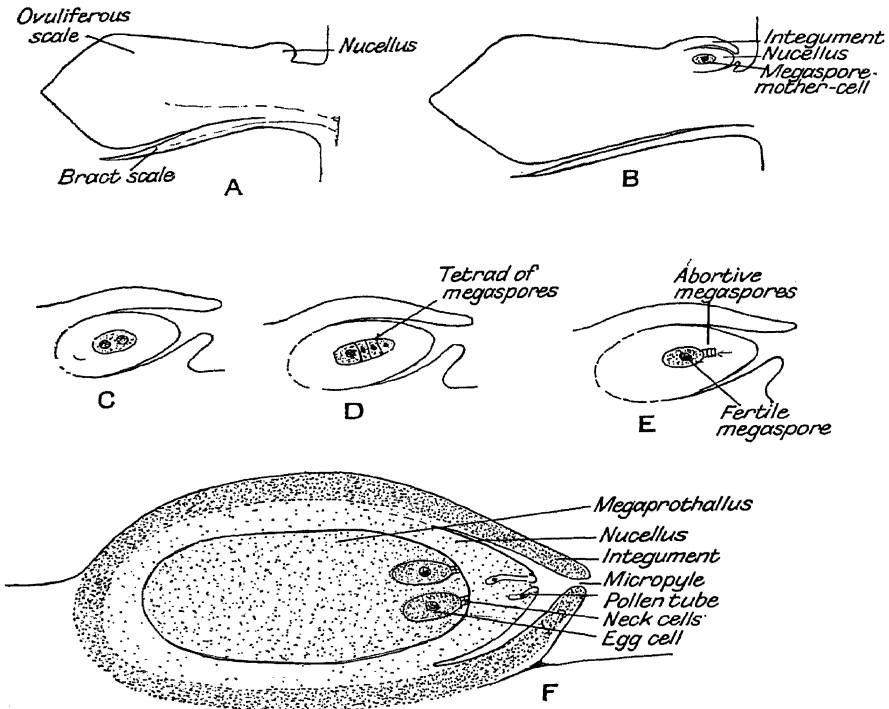


FIG. 83.—*Pinus*.

A–E, development of ovule, to show formation of megaspores; F, longitudinal section through ovule, prior to fertilisation.

two layers of the microspore-coat. The pollen-grains are liberated by the pollen-sac dehiscing along the lower side, and are carried by the wind to the female cones.

At the time of pollen-dispersal, the megasporophylls separate slightly to allow the pollen-grains to be blown between them. The tip of the nucellus of the ovule becomes disorganised to form a drop of fluid which exudes through the micropyle and comes in contact with the pollen-grains. As the fluid dries, it draws the pollen-grains

onto the tip of the nucellus, effecting *pollination*. When pollination takes place, the megaspore, within the ovule, has not started its development, nor does it do so until the next spring, about ten months after pollination. In the meantime the pollen-grain grows out to form a short *pollen-tube* which penetrates the tissue of the

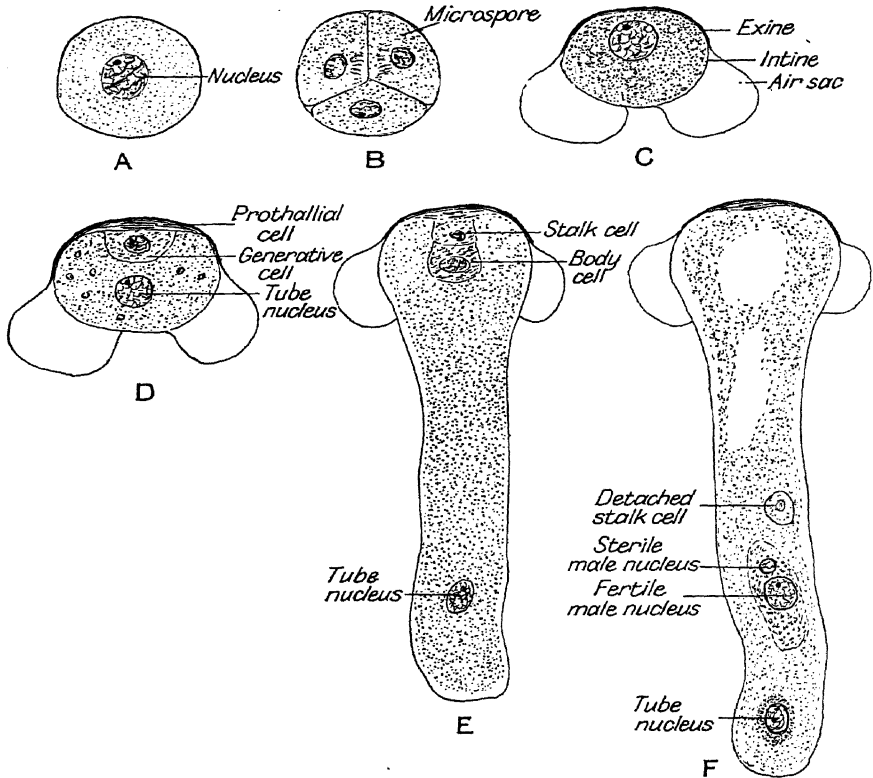


FIG. 84.—*Pinus*.

A, pollen-mother-cell; B, division of A to form microspores; C, later stage of microspore; D, mature pollen-grain at time of dispersal; E, F, development of pollen-tube (microprothallus).

nucellus and enables the microprothallus to live parasitically on the nucellus. The megasporophylls become firmly closed again, and the stalk of the female cone curves downwards. During the summer the female cone enlarges slightly and becomes more woody, but the main part of its growth takes place in the next season.

The germination of the megaspore occurs in the season following

pollination, and the whole of its growth is at the expense of the nucellus which encloses it.

By rapid nuclear division, a large oval megaprothallus is formed inside the nucellus, and about twelve months after pollination several simple archegonia arise at the end nearer the micropyle. The archegonium is much simpler than that of the Male fern, and consists of a short neck, composed of two tiers of four cells each, and a large venter containing an egg-cell, above which is a minute ventral-canal-cell (Fig. 83, F). The megaprothallus is now in a condition for fertilisation to proceed.

As the megaprothallus has been forming, the pollen-tube (= microprothallus) has continued to elongate towards it. The generative cell divides to form a *stalk-cell* and a *body-cell* (Fig. 84, E) which move into the pollen-tube, already occupied by the tube-nucleus. The nucleus of the body-cell divides to form two *male nuclei*, which represent male gametes, although, in *Pinus*, only one is fertile (Fig. 84, F). As it continues to elongate, the tip of the pollen tube ultimately arrives at the megaprothallus, and by breaking through the neck-cells of an archegonium, discharges its contents into the egg-cell. The fertile male nucleus fuses with that of the egg-cell to effect fertilisation and a diploid zygote results.

As a rule, several pollen tubes are developing simultaneously on the nucellus, and as each megaprothallus has several archegonia, more than one of these may be fertilised. The method of fertilisation by means of a pollen tube which carries passive (non-motile) male gametes to the egg-cell is called *siphonogamy*.

The zygote undergoes development enclosed in the megaprothallus, which provides the necessary food, having obtained it from the nucellus which receives it from the parent sporophyte. Shortly after fertilisation, the zygote nucleus divides, and the daughter-nuclei divide to form four nuclei which pass to the inner end of the zygote (Fig. 85, D). Each nucleus again divides and the resulting eight nuclei become separated by walls and form two tiers of four cells each. A final division results in the formation of four tiers of cells, the uppermost nuclei being situated in the cytoplasm of the zygote (Fig. 85, E). This sixteen-celled structure is called the *pro-embryo*.

The cells next to the lowest tier elongate, forming the *suspensors*, and cause the lowest cells to be pushed into the prothallial tissue below the archegonium. In most cases the suspensor-cells separate, and each of the isolated end cells commences to form an embryo (Fig. 85, F, G). It is not uncommon, at this stage of the ovule, for several embryos to be developing together, as several archegonia may have been fertilised, and the same procedure will have gone on

in each zygote formed. The megaprothallus has also undergone enlargement, during this time, at the expense of the nucellus, which is ultimately represented by a thin skin. Before the development of the several embryos has gone very far, one surpasses all others,

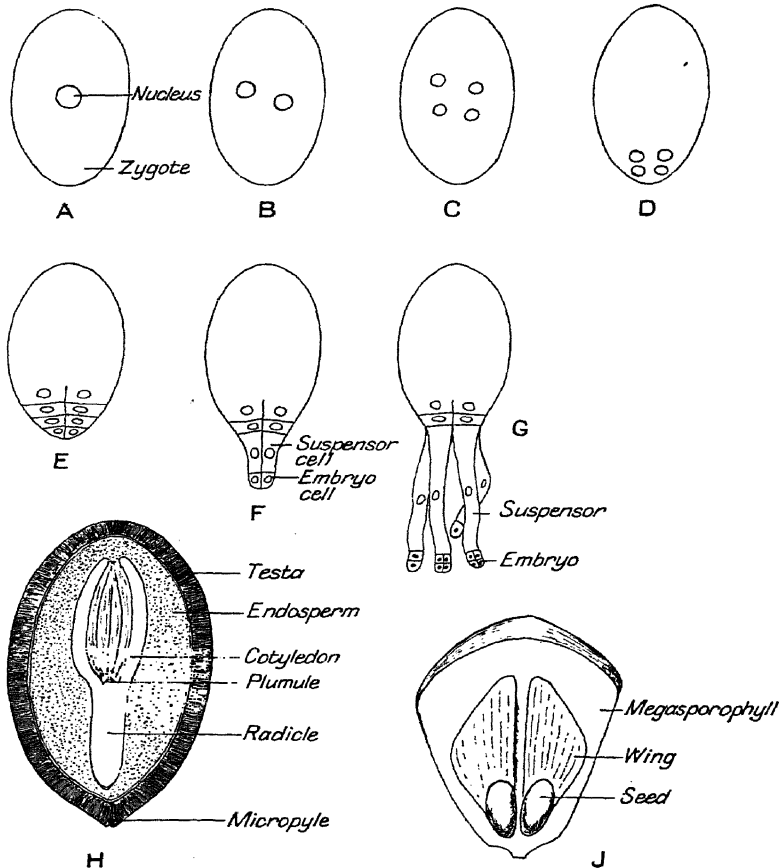


FIG 85.—*Pinus*.

A–G, development of embryo from zygote (description in text); H, longitudinal section of mature seed ($\times 8$); J, single scale of mature female cone ($\times 1\frac{1}{2}$).

which gradually degenerate, the successful embryo continuing its growth to form a radicle, a plumule, and a number of cotyledons. The tissue of the megaprothallus has accumulated food, and formed the storage tissue, or *endosperm*, and the integument has become the resistant *testa* of the mature seed (Fig. 85, H).

The changes from ovule to seed occupy a period of about one year, so that the ripe seeds are not ready for dispersal until two years after the first appearance of the female cones.

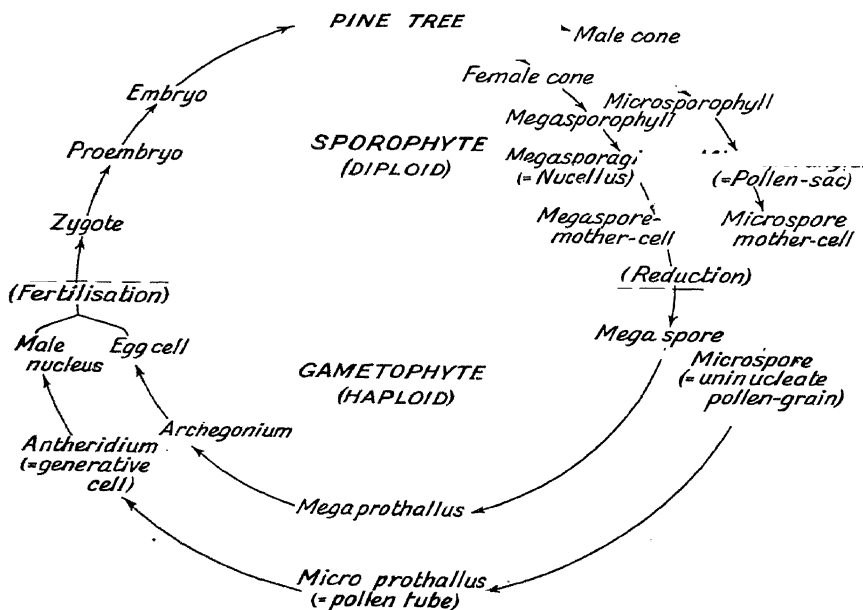
As the ovules ripen, the megasporophylls enlarge considerably to form a cone, about 2 inches long. Lignification then proceeds, so that the scales become woody, but from their upper surfaces thin transparent scales differentiate as attachments to the seeds (Fig. 85, J). As the woody cones dry, the scales separate, and the seeds, together with the wing-like scales, are shed, and carried away by the wind.

The germination of the seed takes place under the usual conditions, and resembles that of endospermic Angiosperm seeds, the cotyledons, in this case, becoming epigeal.

It will now be realised that although the spore and the seed are reproductive bodies, they are not homologous structures.

The mature Pine seed consists of parts of three distinct phases in the life-cycle, viz. parent sporophyte, represented by the integument or testa, female gametophyte, represented by the endosperm, and new sporophyte, represented by the embryo. After germination, the new sporophyte, alone, survives, for the endosperm is absorbed by the developing embryo, and the testa decays.

The life-cycle of the Pine is summarised below.



CHAPTER XVI

SPERMATOPHYTA, 2. ANGIOSPERMÆ. THE FLOWER. POLLINATION. FERTILISATION

The Angiosperms form the greater part of the present vegetation of the world. They are regarded as the culminating point in plant evolution, and have become particularly adapted for survival under terrestrial conditions, both with regard to their vegetative structure and methods of reproduction. Angiosperms have much in common with the Gymnosperms but differ in details of vascular anatomy and seed-formation. Whereas all Gymnosperms are woody perennial plants, the Angiosperms include woody and herbaceous forms, some of which may be annual.

The vascular system of the Angiosperms includes the vessel as the characteristic xylem element, and the companion cell associated with the sieve-tube in the phloem.

In typical Angiosperms, the sporophylls are borne by the same reproductive shoot, which is now known as a *flower*. The microsporophylls take the form of *stamens*, and the megasporophylls are called *carpels*, although this term can also be applied to the megasporophyll of *Pinus*. The ovules of Angiosperms are completely enclosed by the carpel in contrast to their open position in the Gymnosperms. This has necessitated the formation, by the carpel, of a special surface, the *stigma*, for the reception of the pollen-grains which cannot reach the ovule directly as in the Gymnosperms.

The flower is a shoot specialised for reproductive purposes, and its various parts are described as *floral leaves*. The flower is found in similar positions on the shoot as the vegetative branches, being either terminally situated as in the tulip, or in the axil of a leaf, known as a *bract*. The bract may be an ordinary leaf, as in the deadly nightshade, or may be modified in form, as in the dandelion (Fig. 111, A).

The apex of the floral shoot is called the *receptacle*, on which the floral leaves are borne in either a spiral or a whorled arrangement.

The flower-stalk is called a *peduncle*, unless a number of flowers are arranged on a common stem to form an *inflorescence* (Fig. 86),

in which case the stalks of the individual flowers are known as *pedicels*.

Floral leaves differ from vegetative leaves in that they do not usually subtend axillary buds. It does sometimes happen, however, that abnormal, or *atavistic* flowers arise, which possess axillary buds, and serve to confirm the view that floral leaves are homologous to vegetative leaves.

The intimate structure of the flower may show considerable

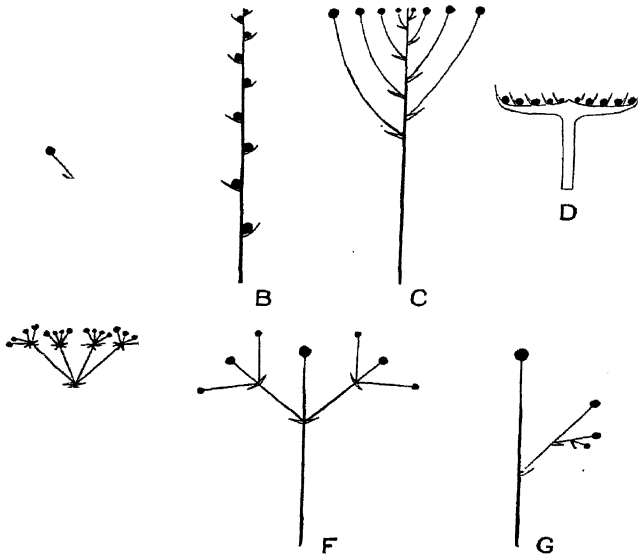


FIG. 86.—Diagrams of some common inflorescences.

Racemose : A, raceme ; B, spike ; C, corymb ; D, capitulum ; E, compound umbel.

Cymose : F, dichasial cyme ; G, monochasial cyme.

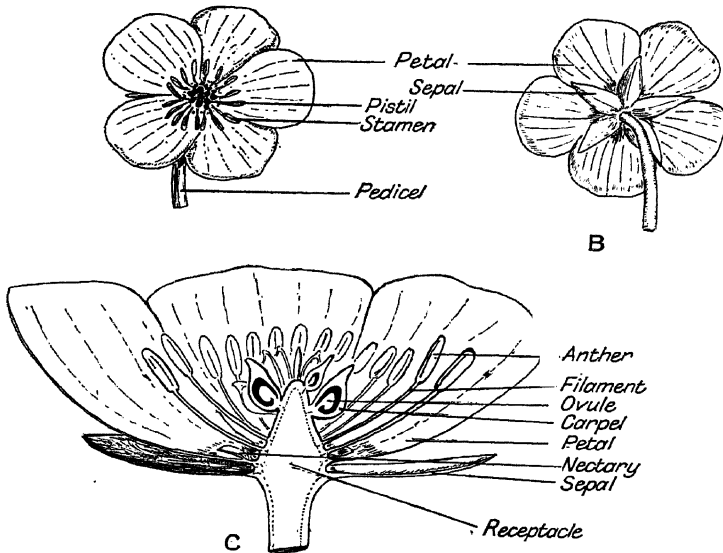
(a = inflorescence axis, b = bract, f = flower.)

variation, according to the species, but fundamentally all flowers are constructed on the same plan.

The typical flower not only bears sporophylls, or *essential organs*, but possesses, in addition, *accessory organs*, called *sepals* and *petals*, concerned partly with the protection of the essential organs, and partly in producing an attractive appearance.

The general structure of a flower may be studied in the buttercup (Fig. 87), the pedicel of which terminates in a short conical receptacle, around which the floral leaves are arranged. The outermost ring, or *whorl*, of floral leaves is the *calyx*, arising at the lowest

level on the receptacle, and consisting of five yellowish green sepals. The calyx serves to protect the inner parts, when the flower is in the bud condition. Above the calyx is the conspicuous **corolla**, composed of five glossy yellow petals alternating with the sepals below. The petals serve as an attraction to insects, owing both to their colour, and to the fact that each bears a small gland, or **nectary**, at its base. The petals and sepals together form the **perianth**, a term used particularly when it is not possible to differ-



G. 87.—Flower of Buttercup (*Ranunculus acris*).

A, front view ($\times 1$); B, back view ($\times 1$); C, half-flower ($\times 2$).

entiate the component whorls as in the flowers of the tulip and the lily, and many of their relatives.

The essential organs, which are the stamens and the carpels, are numerous in the buttercup flower, and are, hence, described as **indefinite**.

The stamens form the **androecium**, and are situated on the receptacle above the petals. Each stamen consists of a head, or **anther**, and a slender stalk, or **filament**.

The carpels, collectively, form the **gynæcium** or **pistil**, and occupy the central part of the flower. Each carpel is a compact body, consisting of a lower swollen **ovary**, containing a single ovule, continued as a short constriction, the **style**, which terminates in a roughened **stigma**.

As the buttercup flower bears both stamens and carpels it is described as *hermaphrodite* or *bisexual*, and as it also possesses a perianth, it is said to be *complete*.

Some Angiosperm flowers bear stamens or carpels only, and are said to be *unisexual*. Flowers possessing stamens only are male,

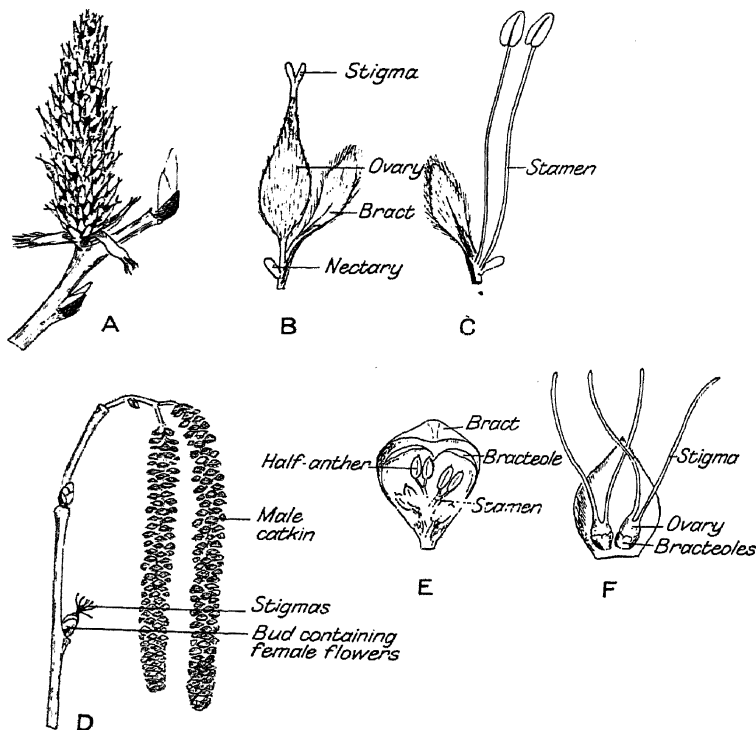


FIG. 88.

A, female catkin of Willow ($\times \frac{1}{2}$); B, single female flower with subtending bract; C, male flower, with bract; D, twig of Hazel bearing male and female inflorescences ($\times \frac{1}{2}$); E, bract with male flower; F, bract with two female flowers. (B, C, E and F, much enlarged.)

or *staminate*, and those possessing carpels only are female, or *pistillate*.

The hazel (Fig. 88, D) produces male and female flowers on the same tree and is described as *monœcious*, whereas the willow (Fig. 88, A) produces unisexual flowers of one sex on distinct trees, and is described as *diœcious*. In both the hazel and the willow the flowers are devoid of perianth, and are *incomplete* and *apetalous*.

Many flowers may exhibit some modification of the perianth, without its complete absence. The usual function of the corolla is to render the flower conspicuous, in connection with the visits of pollinating insects. In the monkshood (*Aconitum*, Fig. 103, B) and the Christmas rose the corolla has become modified to form nectaries which secrete a sugary fluid, **nectar**, as an attraction to insects. The calyx of these flowers has therefore become large and coloured to undertake the attractive function of the reduced corolla, and is described as **petaloid**. Petaloid calyces are also found in *Clematis* and marsh marigold, but in these examples the corolla has completely disappeared.

The general symmetry of the flower is largely decided by the perianth and two types of symmetry are recognised. The flowers of the buttercup, tulip (Fig. 112), and primrose (Fig. 94) can be divided longitudinally into two similar halves in several planes, and are described as **regular**, or **actinomorphic**. On the other hand the flowers of the sweet pea (Fig. 105), monkshood, and larkspur (Fig. 103, D) can be divided symmetrically by one plane only, and are described as **irregular**, or **zygomorphic**, a feature generally associated with insect-pollination.

Other variations in floral structure found in the Angiosperms include the fusion of certain members of the flower. In the buttercup all the organs are **free**, being inserted independently on the receptacle.

The members of one particular whorl may become fused to one another, which is referred to as **cohesion**, and may involve all the floral whorls of one flower. For example, in the deadly nightshade (*Atropa Belladonna*, Fig. 109), the calyx consists of five united sepals, the corolla of five united petals to which the five stamens are attached, and the pistil of two united carpels. The calyx is described as **gamosepalous**, in contrast to the **polysepalous** calyx of the buttercup; the corolla is **sympetalous**, in contrast to the **polypetalous** corolla of the buttercup; the pistil is **syncarpous** in contrast to the **apocarpous** pistil of the buttercup, which is composed of several distinct carpels.

The cohesion of stamens is not of wide occurrence, but it is a characteristic feature of the andrœcium of certain Angiosperm families. In the British members of the family Leguminosæ, which includes the sweet pea, broad bean, gorse, and laburnum, there are ten stamens united in one of two ways by their filaments. In the sweet pea (Fig. 105, c) and broad bean, nine stamens are fused, but one remains free, producing a **diadelphous** andrœcium, which is found in those members of the family possessing nectaries. In the gorse and laburnum all ten stamens are united as a sheath

round the pistil, and the androecium is said to be *monadelphous*. The androecium of members of the family Compositæ, which includes the dandelion, daisy, thistle and groundsel, is characterised by the fusion of the five anthers into a tube, the filaments remaining free. This androecium is described as *syngenesious* (Fig. 111, B).

Adhesion refers to the union of members of different whorls of the flower and the commonest example is the attachment of the stamens to the perianth. In the deadly nightshade and the primrose the stamens are attached by their filaments to the corolla,

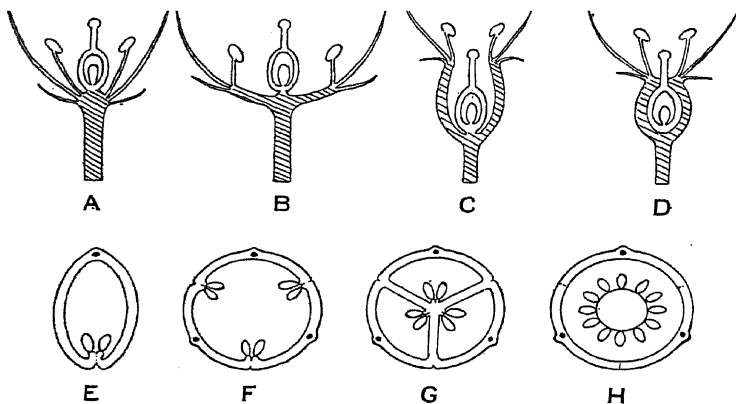


FIG. 89.

A-D, diagrammatic longitudinal sections to show insertion of floral whorls (receptacle shaded).

A, hypogynous; B, C, perigynous; D, epigynous.

E-H, diagrammatic transverse sections of ovary, to show types of placentation.

E, marginal; F, parietal; G, axile; H, free-central.

and are *epipetalous*, whilst in the lily-of-the-valley they are attached to the undifferentiated perianth, and are *epiphyllous*.

The *insertion* of the floral parts on the receptacle, and the nature of the latter, are features of the flower which may be of importance in the classification of Angiosperms.

In the buttercup, the receptacle is conical and its apex is occupied by the pistil, the other floral whorls being inserted at lower levels. The flower is therefore said to be *hypogynous* (Fig. 89, A).

In the strawberry flower, the apex of the receptacle is also occupied by the pistil, but the lower part of the receptacle forms a saucer-like expansion which carries the other whorls of the flower outwards, producing a *perigynous flower* (Fig. 89, B). The perigynous condition occurs also in the rose, the receptacle of

which becomes extremely concave, and almost encloses the ovary portion of the pistil (Fig. 89, c). The receptacle of the apple flower completely surrounds the ovary, and fuses to it, so that the other floral parts are apparently inserted above the ovary, and the flower is *epigynous* (Fig. 89, d).

The nature of the insertion decides the position of the ovary relative to the other parts of the flower. The ovary of the hypogynous and perigynous flowers is said to be *superior*, and that of the epigynous flower, *inferior*.

The origin and development of the stamens and carpels take place whilst the flower is very young, and it is not uncommon to find that the flowers of one season were formed in the previous season. This may be ascertained by examining the dormant bulb of the tulip, or the mixed bud of the horse-chestnut twig during the winter.

The stamen, which is the microsporophyll, originates as an outgrowth of the receptacle, the anther arising first, followed, much later, by the elongation of the filament.

The young anther consists of a solid parenchymatous tissue bounded by an epidermis, and is more or less rectangular in transverse section. At the corners, beneath the epidermis, four longitudinal rows of cells become delimited (Fig. 90, a). These are the *archesporial cells*, each of which divides by a tangential wall (Fig. 90, b). Of the two cells so formed, the inner undergoes division to form a column of sporogenous cells, whilst the outer divides to form a several-layered *endothecium* beneath the epidermis (Fig. 90, c). The endothecium surrounds the sporogenous tissue, and its innermost layer forms a nourishing tapetum. The outermost layer of the endothecium consists of large cells which gradually lose their contents, and their walls become thickened by transverse bands to form the *fibrous layer* (Fig. 90, c).

The sporogenous tissue is composed of pollen-mother-cells (= microspore-mother-cells), each of which undergoes meiosis to form a tetrad of microspores, or immature *pollen-grains*. The pollen-grain is invested with a thin intine and thicker exine which may show spines, ridges or other features on its cutinised surface. Whilst the formation of pollen has been proceeding, the tapetal cells have shrunk, as they supplied nourishment to the pollen-grains.

The anther has now enlarged to maturity, and the filament has become an elongated stalk. The mature anther is a bilobed body, each lobe containing two pollen-sacs (micro-sporangia), and the lobes are joined together by a parenchymatous *connective* in which is a simple vascular bundle, which runs through the filament to the receptacle. The pollen-sac contains the ripe pollen-grains,

surrounded by a wall derived from the endothecium and bounded on the outside by the cutinised epidermis (Fig. 90, H). The endothelial cells, at this time, are dead, and the most prominent feature is the fibrous-layer, previously referred to, which is interrupted, between the pollen-sacs of each lobe, by small thin-walled cells. When the anther opens to liberate the pollen, dehiscence occurs at

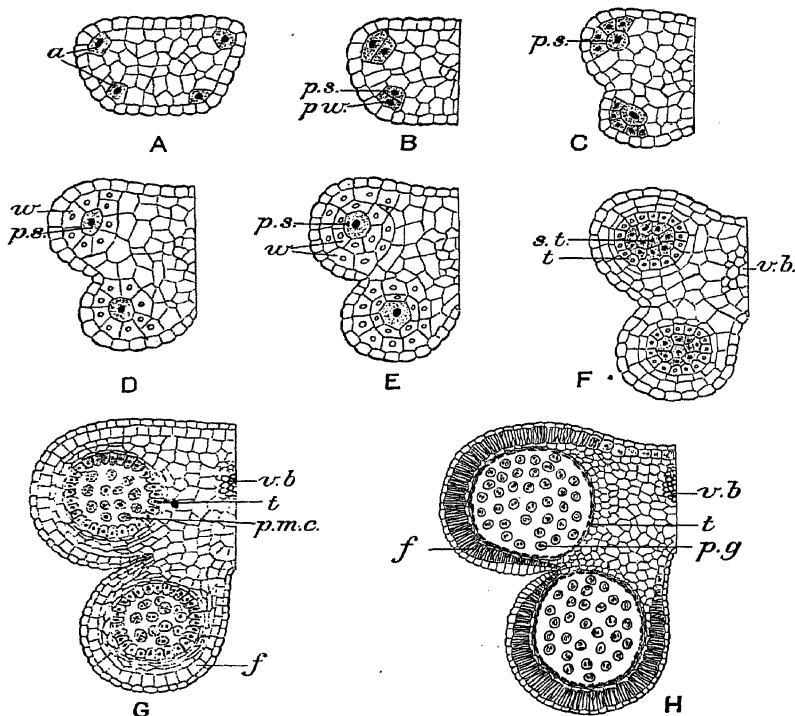


FIG. 90.—Stages in development of Anther.

A, young anther, transverse section; B–H, half-anther, transverse section.

(*a* = archesporial cell, *f* = fibrous layer, *p.g.* = pollen-grain, *p.m.c.* = pollen-mother-cell, initial pollen-sac-cell, *p.w.* = initial wall-cell, *s.t.* = sporogenous tissue, *t* = tapetum, vascular bundle, *w* = wall-cell.)

fibrous-layer. Dehiscence is brought about by the tension of the fibrous-layer, which sets up a tension, eased by the separation of its thin-walled cells, so that the pollen-sacs of the lobe simultaneously burst, and pollen-grains commence the formation of the microgamete before they leave the pollen-sac. The mature pollen-grain consists of two cells, represented by a *tube nucleus*, and a

generative nucleus associated with a small amount of denser cytoplasm (Fig. 91, c).

The carpels arise, like the stamens, as outgrowths of the receptacle, and, as in the pine, are megasporophylls bearing megasporangia in the form of ovules.

Carpels arise in various situations, according to the type of pistil they are to form. Each is originally a small fleshy outgrowth, near to the apex of the receptacle. As it enlarges it forms a cavity which later becomes the central space, or *loculus*, of the ovary.

In the buttercup and the broad bean, the edges of the individual

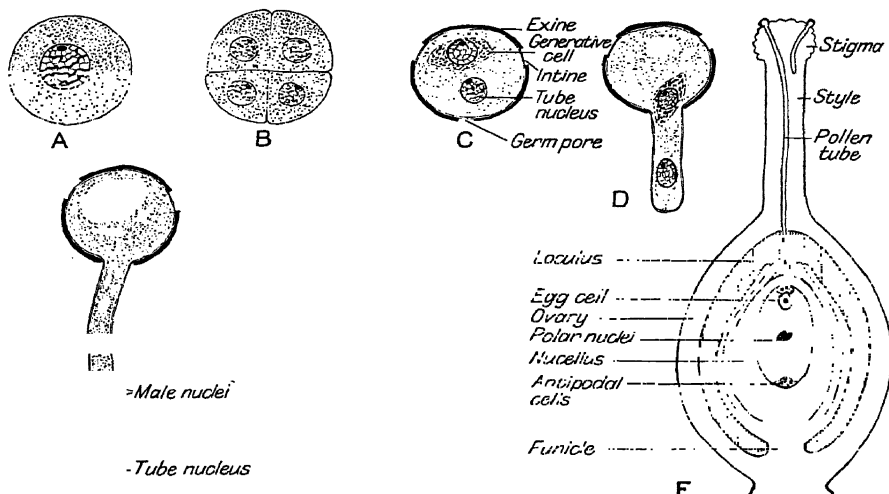


FIG. 91.—Sexual reproduction in Angiosperm.

A, pollen-mother-cell; B, tetrad-division of A; C, mature pollen-grain; D, E, germination of pollen-grain; F, diagrammatic longitudinal section of fertilisation in an orthotropous ovule.

carpels come together and fuse to form a single loculus, but in the tulip which possesses three carpels in each flower, the edges of the adjacent carpels fuse in such a way as to form three compartments which are the loculi of the syncarpous ovary. Many other variations may occur, but in every case the carpels arise singly, and carry out the fusions, which may occur, at a later stage of development. During the early growth of the carpel, it differentiates to form the parts which are found in the pistil. The lower part forms the ovary, and the free end, the stigma, whilst between these two a style of varying length is produced.

In the formation of a syncarpous pistil, the whole of the uniting

carpels may fuse, such as in the tulip and the deadly nightshade, where the union of carpels is indicated by the lobed nature of the stigma, and the *sutures*, or lines down the ovary.

In the dandelion (Fig. 111, c) and the hogweed (Fig. 108, D), fusion involves ovary and style, but the stigmas remain distinct.

The ovules are formed as outgrowths of the infolded margins of the carpels, known as the *placentas*. The number of ovules formed by each carpel varies greatly from plant to plant, being one in the buttercup and several hundred in the foxglove (*Digitalis*).

The arrangement of the ovules in the ovary is called *placentation*, which is typical for a particular species, and follows certain well-defined plans, usually best seen in a transverse section of the ovary.

In the buttercup, the ovule arises from the base of the ovary, and the placentation is *basal*. In the broad bean and the monkshood, several ovules are formed in each carpel, the margins of which fuse together, so that the two placentas form a row of ovules down one side of the ovary, and the placentation is *marginal* (Fig. 89, E). In syncarpous pistils, the number of associated carpels may be two or more, and the placentation is decided by the behaviour of the margins of the united carpels. The three carpels of the tulip fuse in such a way as to carry the placentas into the centre of the ovary, and divide it into three compartments. The ovary is therefore *trilocular* and possesses *axile placentation* (Fig. 89, G).

The violet pistil also possesses three carpels, but they unite to enclose a single locus which bears three double rows of ovules, and has *parietal placentation* (Fig. 89, F). In the mustard and most other members of the family Cruciferae, the two carpels originally exhibit parietal placentation, but early in the growth of the pistil, outgrowths are formed from each placenta across the locus, which becomes divided into two. The primrose pistil consists of five united carpels enclosing a single locus, and the ovules are formed on a central projection arising from the base of the ovary. In transverse section, the ovary appears to consist of an outer wall enclosing a cavity, in the centre of which is a small placenta bearing numerous ovules; the placentation is described as *free-central* (Fig. 89, H).

The development of the ovule is very similar to that of *Pinus*. From the placenta a multicellular nucellus is formed, and from the base of this two integuments commonly develop to enclose it, except for the micropyle at the tip. The development within the nucellus is not uniform throughout the Angiosperms, but in many species, of which the vegetable marrow (*Cucurbita*) is one, megaspore formation proceeds in the following manner. At the apex

of the nucellus a cell with dense contents and a prominent nucleus is delimited hypodermally. This is the archesporial cell, which divides to form an inner sporogenous cell, and an outer tapetal cell which is gradually absorbed by the growth of the sporogenous cell

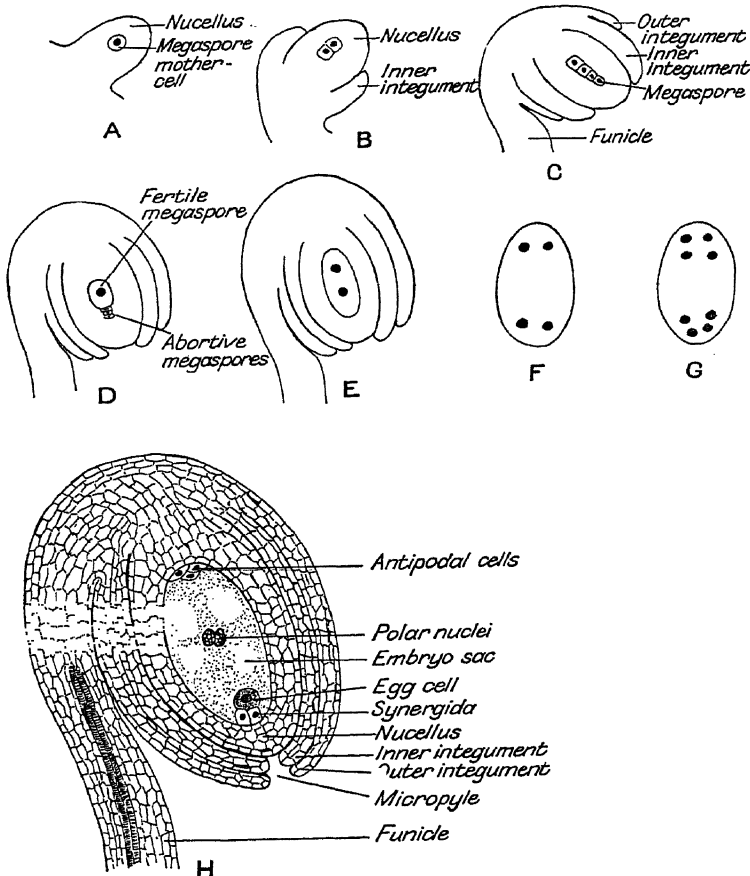


FIG. 92.

A-G, development of female gametophyte (embryo-sac) in ovule of Angiosperm; E-G, stages in nuclear division of megaspore; H, longitudinal section of an anatropous ovule.

(Fig. 92, A). The sporogenous cell represents a single megaspore-mother-cell, which undergoes meiosis to form a linear tetrad of haploid cells, the megaspores (Fig. 92, c). A single megaspore of this tetrad survives and enlarges to become the oval **embryo-sac**-

I, the remaining megaspores breaking down and disappearing (Fig. 92, D).

By the time that the embryo-sac-cell has formed in the nucellus, the ovule has usually produced a stalk, the *funicle*, at the base. The funicle may be short or elongated, and the body of the ovule generally takes up a definite position in relation to it. In some ovaries, such as that of the rhubarb, the ovule remains in the same line as the funicle and is described as *orthotropous* (Fig. 91, F), but in other cases, including the buttercup, the ovule bends so that it lies along the funicle with its apex directed towards the point of attachment to the placenta, and is described as *anatropous* (Fig. 92, H).

Anatropous ovules are very common in Angiosperms, and in some cases the funicle fuses with the integuments, during later growth, to form a ridge, the raphe.

Pollination

When the stamens and pistil are mature, the process of pollination can take place. Pollination, in Angiosperms, consists in the transference of pollen-grains from the anthers to the stigma, not to the ovule direct. It is a stage in the process of fertilisation, but this will only occur if the right kind of pollen is placed on the stigma. The pollen of the anthers of some varieties of apple and pear, and of the red clover may be placed on the stigma of the same flower, but no fertilisation results as the further development of the pollen-grains is prevented. Flowers of this kind are *self-sterile*.

There are two types of pollination, viz. *self-pollination* and *cross-pollination*, and these terms usually are taken to mean that fertilisation will naturally follow.

Self-pollination consists in the transference of effective pollen from the anthers of a flower to the stigma of that flower, and occurs in the sweet pea and the garden pea. It is the simpler method, owing to the close association of the necessary organs. In some plants, including the violet and the wood sorrel (*Oxalis*) fruit-production is restricted to certain minute flowers which never open, and which effect self-pollination within the bud. These flowers are *cleistogamic*.

Cross-pollination involves the carriage of pollen from one flower to the stigma of a distinct flower of the same, or a closely related species. The carriage of pollen is effected under natural conditions by two agencies, wind and insects, and flowers are generally specialised in connection with one or other agent. Pollination by the wind is largely a matter of chance, so that, as a rule, *wind-pollinated*, or *anemophilous* flowers produce large quantities of pollen

and have large stigmatic surfaces to increase the probability of pollination. The hazel (Fig. 88, D) is an example of a plant with anemophilous flowers. It produces its inflorescences early in the year before the leaves appear, so preventing any hindrance to the arrival of pollen on the stigmas. The male inflorescence is in the form of a catkin (Fig. 88, D), which is pendulous when ripe, and bears a series of bracts with simple staminate flowers in their axils. Each male flower (Fig. 88, E) possesses four stamens only; there is no perianth, or nectary. The female flowers are enclosed in certain winter buds, and, at the time of pollination, the scales of the bud open at the apex to allow the pink stigmas to protrude. The female flowers (Fig. 88, F), are borne in pairs by bracts within the bud, and each consists of a pistil having two filamentous stigmas and an ovary surrounded by a number of minute scales or *bracteoles*. Copious pollen is formed by the male catkin, and as the catkin shakes in the wind, the pollen may be blown to the stigmas. Other examples of wind-pollinated flowers are the grasses, which form inconspicuous hermaphrodite flowers with large feathery stigmas, and anthers very loosely attached to slender filaments. Pollen may be carried many miles by the wind and, so long as it remains dry, can effect fertilisation.

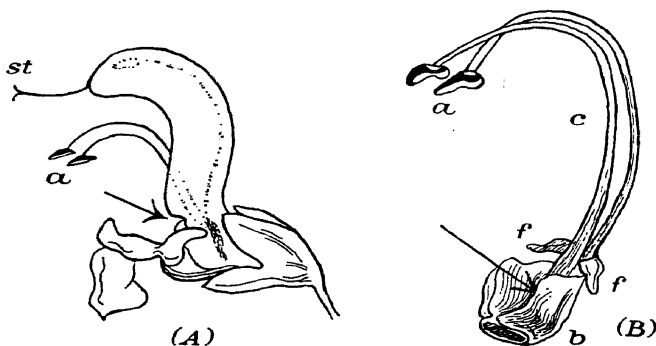
Insects are more certain and economical agents for pollination than the wind, for they generally visit flowers systematically. The insects most concerned with pollination are bees, butterflies and moths. Bees, in particular, are important as they usually confine themselves to one species of plant during a particular journey.

Insect-pollinated, or *entomophilous* flowers commonly possess an attractive scented perianth and produce nectar. The nectar is secreted by nectaries which are so situated as to cause the insect's body to rub against the anthers and stigma of the flower.

There are many interesting forms of floral structure connected with insect-pollination. The sage (Fig. 93) forms a zygomorphic flower which has a tubular two-lipped corolla, at the bottom of which is the ovary and a nectary. A long thin style carries the forked stigma to the throat of the corolla, where it is at first protected by the hooded upper lip. The two epipetalous stamens have anthers specialised into an inner sterile lobe and an outer fertile lobe, and are so affixed to the filaments that the sterile lobe lies across the corolla tube (Fig. 93, B). When a bee visits the flower for nectar, it alights on the lower corolla-lip and forces its body into the corolla-tube. In doing this it pushes against the sterile anther-lobes, which causes the fertile lobes to come down on its back and deposit pollen there. Later, the style of the flower which has shed its pollen, bends to place the stigma across the throat of the flower,

so that, when an insect bearing pollen arrives at the flower, the stigma will be brushed against and thus receive pollen.

Some flowers are dependent on one particular insect to effect pollination. This is the case in an American plant, *Yucca*, which can only be naturally pollinated by a small moth, *Pronuba*. The stigmatic surface of the *Yucca* flower is confined to a canal down the style. *Pronuba* arrives at the flower in order to lay her eggs, but before doing so she collects a ball of pollen from the anthers. The moth then pierces the ovary-wall with her ovipositor and lays eggs amongst the ovules, after which she ascends the style and forces the ball of pollen into the stigmatic canal, instinctively to provide food for the grubs which will hatch from the eggs. Thus pollination



g. 93.—Pollination of Sage (*Salvia*).

A, side view of flower—dotted line represents position of stamens beneath upper lip of corolla ($\times 1$); B, stamens removed from flower ($\times 2$), arrow indicates point of pressure of insect's head.

(a = fertile anther-lobe, b = sterile anther-lobe, c = connective, f = filament, st. = stigma.)

is effected, and although the larvæ, from the eggs laid in the ovary, eat some of the ovules, there are sufficient ovules left to form mature seeds.

Certain types of floral structure are found which ensure cross-pollination and prevent self-pollination.

The production of unisexual flowers is one of the simplest devices. In the hazel, pollen transference is effected by the wind, but in another catkin-forming plant, the willow (Fig. 88, A), insects carry the pollen, being attracted to the male and female catkins by the nectar and the scent produced there.

In the primrose (Fig. 94) and the cowslip, two kinds of flower are produced on different plants. Both kinds are complete and of the same general appearance, being called '*pin-eyed*' and '*thrum-eyed*' respectively. They each possess stamens and pistil, but in

the 'pin-eyed' form the pistil has a long style, which carries the globular stigma to the throat of the long corolla-tube, whereas the style of the 'thrum-eyed' form is short and the stigma is half-way up the corolla-tube (Fig. 94, B). On the other hand, the epipetalous stamens of the 'thrum-eyed' flower are at the throat of the corolla, whilst those of the 'pin-eyed' flower are half-way down the corolla-tube. Thus, the anthers of one flower are at the same level as the stigma of the other type. Pollination is usually effected by moths with long probosces. They alight on the flat part of the corolla and uncoil their probosces to get at the nectar secreted at the bottom of the corolla-tube. They therefore carry pollen away from one flower, at the correct level on the proboscis for transference to the stigma of the next flower of the other type which they visit. Flowers of this type are described as *dimorphic*.

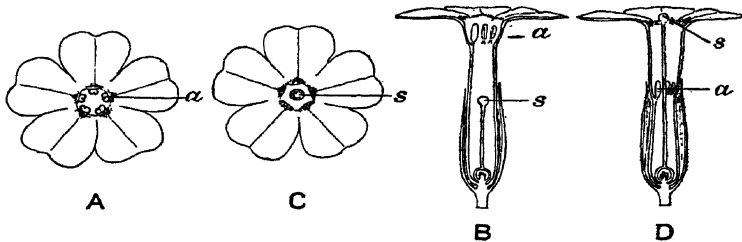


FIG. 94.—Dimorphic Flowers of Primrose.

A, thrum-eyed (short-styled) flower, in plan; B, half-flower of same; C, pin-eyed (long-styled) flower, in plan; D, half-flower of same (all $\times \frac{1}{2}$).

(a = anther, s = stigma.)

Some hermaphrodite flowers prevent self-pollination by the ripening of the two sets of essential organs at different times, a condition called *dichogamy*. In the figwort (Fig. 95, A, B) the zygomorphic flower is pollinated by bees and wasps which thrust their bodies into the flower in their search for nectar. The stigma is receptive before the anthers of the same flower are ripe, so that in younger flowers the style holds the stigma across the throat of the flower, in a suitable position to receive pollen. After pollination, the style withers and droops over the lower lip of the corolla, and the filaments of the stamens then elongate and carry the anthers across the throat of the flower.

Another example is found in the common plantain (Fig. 95, c, D), in which the filaments are bent downwards until the stigma has been pollinated, when they become erect and expose the ripe anthers. Flowers in which the stigma ripens before the stamens are described as *protogynous*, a condition which is found in many grasses, in addition to the plants described.

In the sunflower, dandelion and most common members of the family Compositæ, the stamens ripen before the stigma of the same flower, and the flowers are **protandrous**. For example, the tubular florets of the sunflower (Fig. 110, c-g) have five epipetalous synergensious stamens, the anthers of which are united into a tube. In the young floret the short style, bearing the closed stigma, is enclosed within the anther-tube. The anthers ripen first and shed

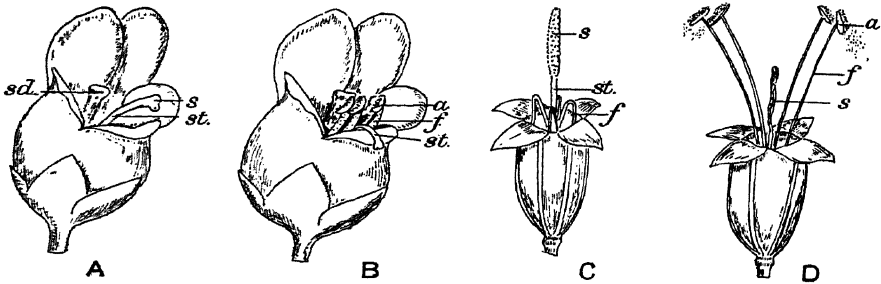


FIG. 95.—Protogynous Flowers.

A, Figwort (*Scrophularia*), in female condition; B, in male condition ($\times 3$); C, Plantain (*Plantago*), in female condition; D, in male condition ($\times 4$).

(a = anther, f = filament, s = stigma, sd. = staminode, st. = style.)

their pollen inwards, so that as the style elongates, it carries the pollen to the top of the anther-tube. The pollen may then be transferred by insects to older florets. Later, when the style projects beyond the anther-tube, the stigma opens to expose the receptive surface, which can then receive pollen from a floret in the younger condition.

Another example of a protandrous flower is the sage, described earlier in the chapter.

Fertilisation

The development of the microspore and megaspore of the Angiosperms follows closely that of the same structures of *Pinus*.

It has already been mentioned that the formation of the microprothallus, consisting of only two cells, commences in the pollen-sac, and is represented by the mature pollen-grain. The pollen-grain is in this two-celled condition when it arrives on the stigma.

The megaspore (= embryo-sac-cell) completes the whole of its development inside the nucellus. The development of the megaspore of *Cucurbita*, which is similar to that of many other Angiosperms, may be taken as an example. In this, the nucleus of the embryo-sac-cell divides and the daughter-nuclei pass to the opposite ends of the cell (Fig. 92, E). They there continue division until

each forms a group of four nuclei (Fig. 92, α). At the micropylar end of the original cell, three nuclei become associated with cytoplasm and form a group of cells, the *egg apparatus*, whilst at the other, or *antipodal* end, three nuclei form a group of small *antipodal cells*. The structure is now the megaprothallus or *embryo-sac*. The nuclei from each pole, which have not been concerned in cell-formation, pass to the centre of the embryo-sac, where they lie side by side to fuse at a later stage in the formation of the *primary endosperm nucleus* (Fig. 92, η).

The egg apparatus consists of a large *egg-cell* and two smaller *synergidæ*. It is often regarded as a simple archegonium, the synergidæ constituting a neck, but another view is that all three cells represent female gametes of which only one, the egg-cell, is fertile.

The other cells of the embryo-sac probably represent vegetative prothallial cells.

The formation of the embryo-sac takes place comparatively quickly, sometimes occupying a few days, which contrasts greatly with the extended development in *Pinus*.

When the pollen-grain arrives on the stigma, it sends out a pollen-tube, usually through a thin part, or *germ-pore*, of the exine. The pollen-tube (Fig. 91, δ) passes down the style, by which it is nourished during elongation. The tube-nucleus and generative cell pass into the pollen-tube, where the generative cell divides to form two *male nuclei* which are both fertile (Fig. 91, ε). Continuing its elongation, the tip of the pollen-tube, in due course, reaches the micropyle of the ovule, either having passed across the loculus of the ovary to do so, or having passed in the ovary-wall, to emerge close to the micropyle.

The tip of the pollen-tube penetrates the apex of the nucellus and passes to the embryo sac (Fig. 91, f). Here it ruptures a synergida, its tip opens and permits the nuclear contents to pass into the embryo-sac. One of the male nuclei passes to the egg-cell nucleus, fuses with it, so effecting fertilisation and forming the zygote. The other male nucleus proceeds to the primary endosperm nucleus with which it fuses to form a *triploid* ($3x$) *endosperm nucleus*. This second fusion, called *xenia*, is mainly of interest in that it makes possible the hybridisation, or mixing, of the characters of the endosperm in seeds such as the cereals, by means of cross-pollination.

It should be noted that the ovary may contain numerous ovules, and each will be fertilised by a distinct pollen-tube, so that many pollen-tubes may be growing in the style at the same time.

The zygote starts to develop as soon as it is formed, and its

growth is accompanied by the division of the endosperm nucleus to form endosperm cells. The details of zygote development depend on whether the plant is Dicotyledon or Monocotyledon, and on the nature of the seed which is to be formed.

In the shepherd's purse, an annual Dicotyledon weed with non-endospermic seeds, the development of the seed from the fertilised ovule is as follows. The zygote divides into two (Fig. 96, B), the outer of which is a large **basal cell** which plays no further part in

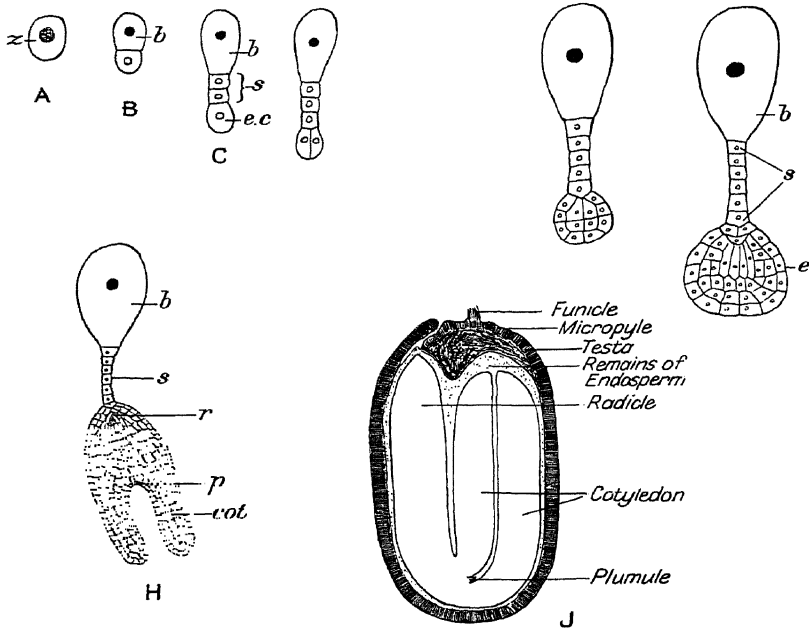


FIG. 96.

A-H, stages in embryology of a Dicotyledonous Angiosperm (*Capsella*); J, longitudinal section of mature seed (enlarged).

(*b* = basal cell, *cot.* = cotyledon, *e* = embryo, *e.c.* = embryo-cell, *p* = plumule, *r* = radicle, *s* = suspensor, *z* = zygote.)

the development. The inner cell continues to divide until it has formed a short chain of cells, the **pro-embryo**, which consists of the **embryo-cell**, at the end remote from the basal cell, and the **suspensor** (Fig. 96, c). The slight elongation of the suspensor serves to push the embryo-cell further into the endosperm, where it will be more satisfactorily nourished.

During the development of the pro-embryo the endosperm has been formed at the expense of the nucellus which disappears com-

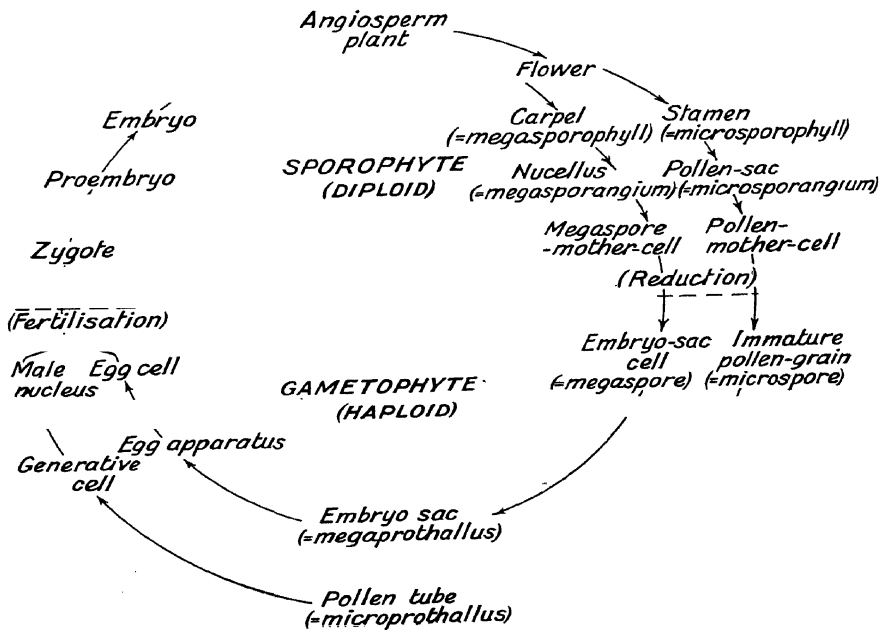
pletely as the seed is formed. The endosperm, however, is also absorbed by the embryo, which has been formed by the division of the embryo-cell. The embryo consists of a radicle and two cotyledons, between which a small plumule is situated (Fig. 96, J). The integuments of the original ovule have by this time formed a resistant testa which, when the seed has completed its growth, encloses the embryo only.

The procedure in the shepherd's purse is the usual type in all non-endospermic seeds. In endospermic seeds, such as the castor oil and the maize, the endosperm is not absorbed by the embryo during formation, but survives as a food-storage tissue in the mature seed. In some seeds, including the black pepper, not only does the endosperm remain as part of the seed, but the nucellus also is present as a food-storing tissue, the *perisperm*, outside the endosperm.

On the ultimate germination of the seed, the embryo develops to form the new sporophyte, and in its early growth it absorbs the other tissues which may be present in the seed, for nourishment.

Therefore there is very little difference between the various types of seed, for in all cases the nucellus and endosperm are absorbed by the embryo, and it is a matter of time as to when this occurs.

The life-history of the typical Angiosperm is summarised below.



CHAPTER XVII

ANGIOSPERMÆ. THE FRUIT. THE DISPERSAL OF FRUITS AND SEEDS

The immediate result of fertilisation in the Angiosperm flower is the enlargement of the ovule to form a seed, but other changes involve the growth of the ovary to accommodate the ovules, which results in the formation of the structure called the *fruit*. When the ovary, alone, ripens, a *true fruit* is produced, but it happens, in some flowers, that parts additional to the ovary enlarge during fruit-formation to produce a *compound*, or *false-fruit*.

In the formation of a true fruit the ovary-wall becomes the *pericarp* or fruit-wall, which, when ripe, may be either tough and dry, or fleshy, and on this character fruits can be classed as *dry* or *succulent*.

Dry Fruits.

The pericarp of the dry fruit may be of a leathery texture as in the sweet pea, or hard and woody as in the hazel.

Dry fruits are conveniently subdivided, on the method of seed-dispersal they adopt, into *indehiscent*, *dehiscent* and *schizocarpic* classes.

Indehiscent dry fruits do not split open to liberate their seeds, but are shed completely from the plant. As a rule, such fruits contain a single seed, which germinates within the pericarp, which is burst open as the radicle elongates. There are a number of distinct types of indehiscent dry fruit.

The fruit formed by the apocarpous pistil of the buttercup and the avens (*Geum*) is a collection, or *etaerio*, of *achenes* (Fig. 97). Each achene is formed from an individual carpel, and has a leathery pericarp enclosing a single seed.

The *samara* is a winged indehiscent dry fruit formed by the ash (Fig. 97, E) and the elm (Fig. 97, F). It is produced from a syncarpous pistil of two carpels, which form a wing-like expansion as they ripen; it contains a single seed.

The *cypsela* is the characteristic fruit of the family Compositæ, exemplified by the dandelion (Fig. 97, G) and the sunflower (Fig.

97, H). It is formed from the inferior ovary of a bicarpellary unilocular syncarpous pistil, and contains one seed. In many cases, such as the dandelion, thistle and groundsel, the calyx persists as a plume of hairs, or *pappus*, which facilitates wind-dispersal of the fruit.

The *caryopsis* is the characteristic fruit of all members of the grass family, Graminaceæ, and is represented by the maize grain

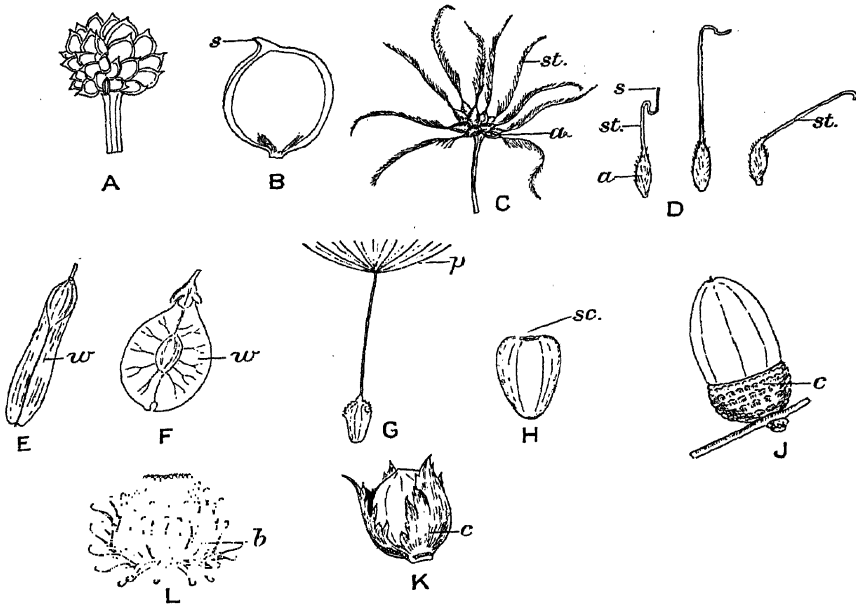


FIG. 97.—Dry Indehiscent Fruits.

A, etaerio of achenes (Buttercup, $\times 2$); B, single achene ($\times 10$); C, plumed achenes (*Clematis*, $\times \frac{1}{2}$); D, achenes of *Geum*, with hooked style ($\times 2\frac{1}{2}$); E, samara (Ash, $\times \frac{1}{2}$); F, samara (Elm, $\times \frac{1}{2}$); G, cypsela (Dandelion, $\times 1\frac{1}{2}$); H, cypsela (Sunflower, $\times 1$); J, nut (Oak, $\times \frac{3}{2}$); K, nut (Hazel, $\times \frac{1}{2}$); L, involucre enclosing cypselas (Burdock, $\times \frac{1}{2}$).

(*a* = achene, *b* = hooked bract, *c* = cupule, *p* = pappus, *s* = stigma, *sc.* = scar of style, *st.* = style, *w* = winged pericarp.)

described in Chapter III. It is formed from a single carpel which encloses one ovule, and as the seed is formed it fills the entire locus so that its testa fuses with the inner layer of the pericarp.

The *nut* is an indehiscent dry fruit with a woody, or tough, pericarp. It is formed from a syncarpous ovary and usually contains a single seed. Examples include the hazel nut (Fig. 97, K)

and the acorn (Fig. 97, J), both of which are associated with a cup-like structure of bracteoles forming a *cupule*.

Dehiscent dry fruits are generally many-seeded, so that they must split open, or *dehisce*, to scatter their seeds efficiently. Dehiscence takes place whilst the fruit is attached to the parent

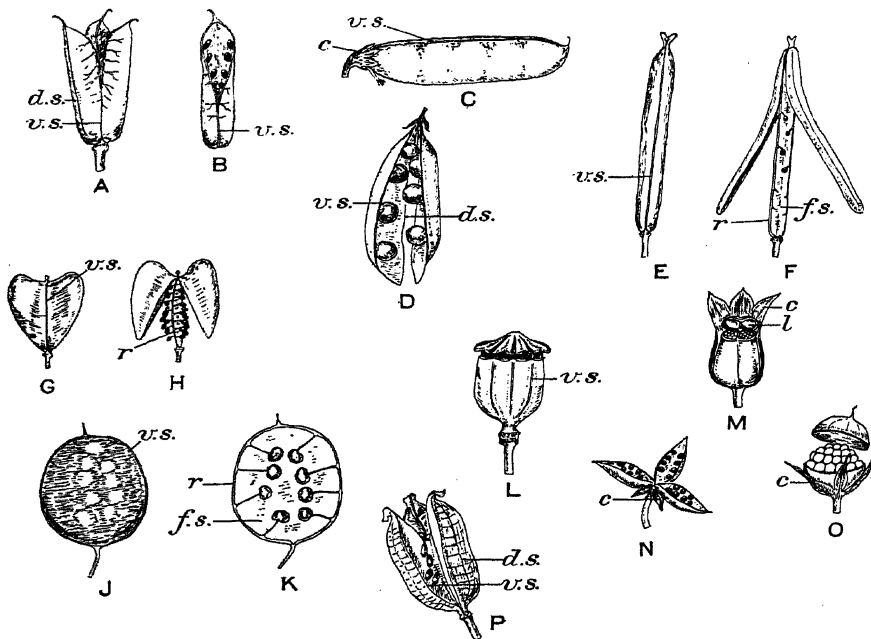


FIG. 98.—Dry Dehiscent Fruits [$\times \frac{1}{2}$ except C, D ($\times \frac{1}{3}$), G, H ($\times 3$), O ($\times 1$)].

A, etecrio of follicles (Larkspur); B, dehiscing follicle; C, legume (Pea); D, dehiscing legume; E, silique (Wallflower); F, silique dehiscing; G, silicula (Shepherd's Purse); H, silicula dehiscing; J, silicula (Honesty); K, dehiscing silicula; L, capsule dehiscing by pores (Poppy); M, capsule dehiscing by lid (Henbane); N, capsule splitting into valves (Violet); O, capsule dehiscing by lid (Pimpernel); P, capsule with loculicidal dehiscence (Tulip).

(c = persistent calyx, d.s. = dorsal suture, f.s. = false septum, l = lid, r = replum, v.s. = ventral suture.)

plant, on which the remains of the fruit will be found, after the seeds have been shed.

The fruit of the monkshood and the larkspur (Fig. 98, A) is an etecrio of *follicles* formed by an apocarpous pistil. Each carpel contains several seeds which are liberated by the follicle splitting down the margin to which the seeds are attached, known as the *ventral suture*.

The characteristic fruit of the family Leguminosæ is the *legume* or *pod* (Fig. 98, c), formed from a monocarpillary pistil which contains several ovules. When ripe the legume splits down the ventral suture, but also along the mid-rib, or *dorsal suture*, of the carpel (Fig. 98, d). In the legumes of the laburnum, vetch, and other members of the family, the two half-carpels, or *valves*, twist after dehiscence and aid the ejection of the seeds.

The fruits formed by the members of the family Cruciferæ are very characteristic dehiscent types. The pistil which forms them is bicarpellary and syncarpous, and although the placentation is parietal, outgrowths form across the single loculus, which is divided into two by a *false-septum*. Two types of dehiscent dry fruit are found in the family, differing mainly in their dimensions. The fruit of the wallflower (Fig. 98, e) and the mustard (Fig. 1, d) is longer than it is broad, being called a *siliqua*, whereas in the shepherd's purse (Fig. 98, g) and honesty (*Lunaria*, Fig. 98, j) it is as broad as it is long, and is called a *silicula*. The dehiscence of the siliqua and the silicula is very similar. When ripe the two carpels separate at the bottom and open upwards, leaving the false-septum attached to the flower-stalk, surrounded by a framework, the *replum*, which represents the placentas. The seeds may remain attached to the replum, from which they will fall later. In the silicula of the honesty the false-septum is parallel to the flat carpels, but in the shepherd's purse it is at right angles to the concave carpels.

A dehiscent dry fruit formed by many diverse plants, and varying considerably in detail, is the *capsule*. It is formed from a syncarpous pistil of two or more carpels, and usually contains numerous seeds. The capsule of the foxglove consists of two carpels, that of the lily and the violet, three, that of the willow-herb four, of the primrose five, and of the poppy many. The capsule may be formed from both superior and inferior ovaries, and with the exception of the willow-herb, which has an inferior ovary, the examples mentioned are formed from superior ovaries. The dehiscence of the capsule also exhibits great variety. It may involve a separation of carpels, as in the violet (Fig. 98, n), or opening by a series of teeth as in the campion, or the formation of holes through which the seeds are shed, as in the poppy (Fig. 98, l), or the formation of a lid which splits off, as in the pimpernel (Fig. 98, o) and the henbane (*Hyoscyamus*, Fig. 98, m).

Schizocarpic dry fruits combine, to some extent, the features of the other two types, as they break up, when ripe, into a number of indehiscent one-seeded portions.

Several members of the family Leguminosæ including, the horse-

shoe vetch (*Hippocrepis*), and species of *Acacia* and *Astragalus*, form a pod-like schizocarp called a **lomentum** (Fig. 99, A, B). The pericarp becomes constricted between the individual seeds, and breaks up into a number of one-seeded parts.

The fruit of the family Labiatæ, which includes the mint, sage, and deadnettle, is a **carcerulus**. This is formed from a bilocular ovary of two carpels, each carpel producing two ovules.

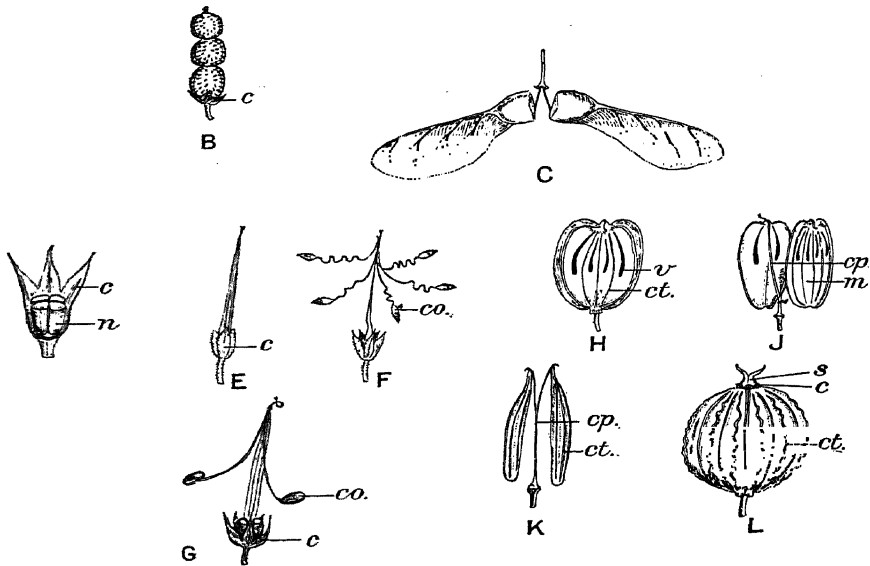


FIG. 99.—Schizocarpic Fruits.

A, lomentum (Radish, $\times \frac{3}{4}$); B, lomentum (*Hedysarum*, $\times \frac{1}{2}$); C, double-samara, dividing (Sycamore, $\times \frac{1}{2}$); D, carcerulus (Deadnettle, $\times 1\frac{1}{2}$); E, regma (*Erodium*, $\times \frac{3}{4}$); F, ditto, cocci separating; G, regma (Cranesbill, $\times \frac{1}{2}$); H, cremocarp (Hogweed, $\times 1\frac{1}{2}$); J, ditto, mericarps separating; K, cremocarp separating (*Myrrhis*, $\times \frac{1}{2}$); L, cremocarp (Coriander, $\times 5$).

(c = persistent calyx, co. = coccus, cp. = carpophore, ct. = costa, m = mericarp, n = nutlet, s = stylopod, v = vitta.)

During the early growth of the ovary, each carpel becomes infolded between the ovules so that four compartments, each containing an ovule, are formed. The resultant fruit consists of four one-seeded indehiscent **nutlets** enclosed in the persistent calyx (Fig. 99, D).

The fruit of the family Umbelliferae is a schizocarp, called a **cremocarp**, formed from an inferior ovary of two carpels. The two carpels are separated by a transverse wall, or **commissure**,

and each loculus contains a single ovule. As the fruit ripens, the ovules enlarge and completely fill the loculi, and a longitudinal strand of fibres, the *carpophore*, develops in the commissure. When ripe the fruit separates into two one-seeded *mericarps*, which remain attached, for a short time, to the fibrous carpophore. Numerous examples of the cremocarp are used in pharmacy, including such drugs as anise, caraway, fennel, dill and hemlock. The ripe mericarp is usually characterised by five longitudinal ridges, or *costæ*, on its surface, and between the ridges are oil canals or *vittæ* (Fig. 99, H).

The fruit of the sycamore (Fig. 99, c) and maple is a *double-samara* formed from two carpels which form wing-like expansions as the fruit ripens. The fruit separates into two one-seeded mericarps.

The fruit of the stork's bill (*Erodium*) is a *regma* formed from a syncarpous pistil of five carpels. The carpels consist of a lower ovary, and a beak-like stylar portion terminated by the stigmas. When ripe the individual carpels, each enclosing one seed, separate by the twisting of the styles, which finally jerk the carpels from the elongated receptacle (Fig. 99, F). A similar fruit is found in the cranesbill (*Geranium*), but in this case the fruitlets, or *cocci*, are dispersed by a spring-like movement of the styles (Fig. 99, G).

Succulent Fruits.

Succulent fruits are almost invariably indehiscent, although the squirting cucumber (*Ecballium*), explodes to liberate its seeds.

There are three types of succulent fruit, viz. the *drupe*, the *drupel*, and the *berry*.

The drupe is a succulent fruit in which the pericarp is differentiated into three clearly defined layers of different texture. The cherry (Fig. 100, A) is a typical example, which is formed from a monocarpillary pistil. The outer layer of the pericarp is a thin coloured skin, the *epicarp*, within which is a thick fleshy *mesocarp*, which becomes sweet and juicy as it ripens, whilst the innermost layer is a woody *endocarp*, or 'stone,' which protects the enclosed seed.

Drupe of similar type are found in the plum, sloe and almond, although in the last, the mesocarp does not become succulent, but splits, when ripe, to release the endocarp with its contained seed.

Drupe are usually one-seeded, but that of the elder (wrongly called a berry) contains a number of seeds, each with its own endocarp, the whole being embedded in the succulent mesocarp. Reference must be made here to the fruit of the coco-nut palm,

which is called a *fibrous drupe*, for, although a dry fruit, it shows a differentiation of the pericarp of somewhat similar type to that of a drupe. The pericarp has an outer cutinised epicarp, a fibrous mesocarp, and a hard endocarp which encloses the large hollow seed.

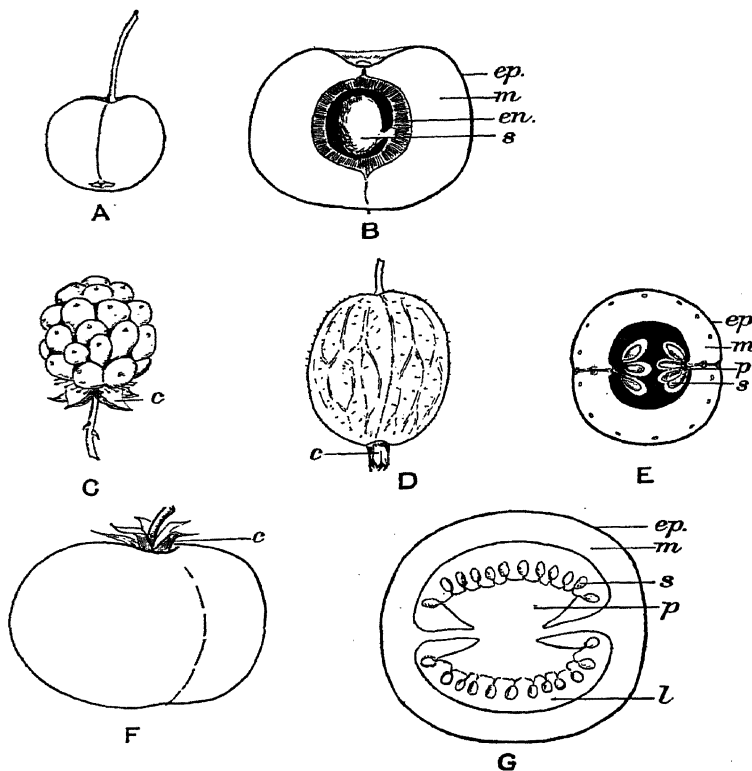


FIG. 100.—Succulent Fruits.

A, drupe (Cherry, $\times \frac{1}{2}$); B, ditto, L.S. ($\times 1$); C, etaerio of drupels (Blackberry, $\times 1$); D, berry (Gooseberry, $\times \frac{2}{3}$); E, ditto, T.S.; F, berry (Tomato, $\times \frac{1}{2}$); G, ditto, T.S.

(c = persistent calyx, en. = endocarp, ep. = epicarp, l. = loculus, m = mesocarp, p = placenta, s = seed.)

Drupels are small drupes formed by the single carpels of apocarpous pistils, in such plants as the blackberry (Fig. 100, c) and raspberry. The pericarp of the drupel is differentiated in exactly the same way as that of the drupe.

The berry differs from the drupe in that it possesses no hard

endocarp, the seeds being protected by hard testas, and embedded in a juicy pulp.

The berry holds the position amongst succulent fruits that the capsule holds amongst dry fruits, as it may be formed of a varying number of carpels, and from superior or inferior ovaries. The berry of the deadly nightshade and the tomato (Fig. 100, F) are formed by superior ovaries, whilst the gooseberry (Fig. 100, D) is formed from an inferior ovary.

The date is a single-seeded berry, the seed being a hard solid structure, owing to the endosperm walls being of hemicellulose.

The orange and the lemon are berries formed from an indefinite number of carpels, having axile placentation. The outer portion of the pericarp is a tough skin which contains numerous oil glands. The succulent part of these fruits consists of succulent hair-like cells, which grow out from the lining of the loculus which they fill completely.

Compound Fruits.

In many species, the ripening of the ovary is accompanied by the enlargement of the receptacle which results in the formation of a false-fruit. This happens in a number of well-known fruits such as the strawberry, apple and pear.

The strawberry (Fig. 101, A) consists mainly of a red fleshy receptacle bearing on its surface the true fruits which are achenes.

In the apple (Fig. 101, D) and pear, the receptacle of the epigynous flower enlarges and becomes succulent as the ovary ripens. The true fruit in this case is indicated by the 'core,' the tough part of which is the main part of the pericarp. This type of fruit is called a *pome*. The fruit of the rose (Fig. 101, B), known as a *hip*, consists of a fleshy concave receptacle enclosing a number of achenes, whilst the hawthorn fruit, or *haw* (Fig. 101, G), is very similar to a pome, but the fleshy receptacle encloses one or more woody achenes.

In the mulberry the perianth takes part in the formation of the false-fruit, which is formed from an entire female inflorescence and resembles, superficially, an etaerio of drupels. As the ovary ripens, the four perianth segments of each female flower become succulent and enclose the true fruit which is a nut.

In the fig the succulent part of the false-fruit is the hollow inflorescence axis which bears on its inner surface the fruits (drupes) formed by the female flowers.

The Dispersal of Fruits and Seeds

The majority of flowering plants produce more seeds than are likely to find suitable conditions for germination owing to the great

competition which exists between species. The chances of the survival of a species are enhanced if the seeds are dispersed over a wide area.

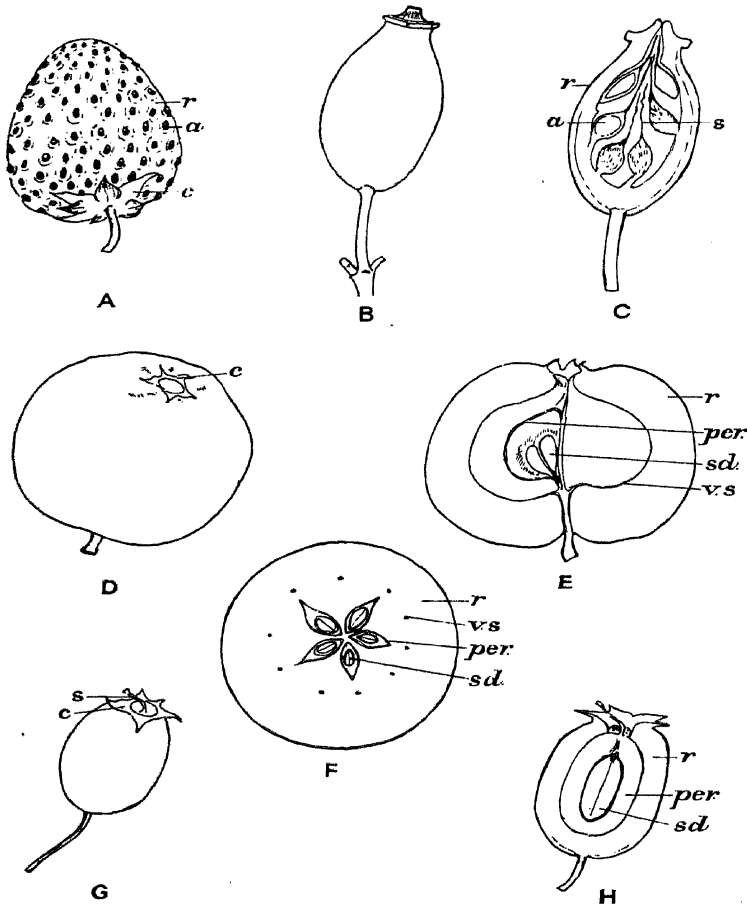


FIG. 101.—False Fruits.

A, Strawberry ($\times 1$); B, Rose hip, external ($\times 1$); C, longitudinal section of B; D, Apple (pome, $\times \frac{1}{2}$); E, longitudinal section of D; F, transverse section of D; G, Hawthorn (haw, $\times 1$); H, longitudinal section of G.

(*a* = achene, *c* = calyx, *per.* = pericarp, *r* = receptacle, *s* = style, *sd.* = seed, *v.s.* = vascular strand.)

There are a number of natural methods of fruit and seed dispersal which vary in efficiency.

Dispersal by Wind.

The wind is a very efficient agent and may carry fruits and seeds long distances.

Wind-dispersed fruits are generally characterised by the possession of wings or hairs which make them light and produce a larger area for the wind to act on.

Winged fruits include the samara of the ash, and the double-samara of the sycamore, both of which are borne on tall trees. When the fruits are shed they fall slowly and drift some distance from the parent tree.

Plumed fruits possess hairy outgrowths. They include the achenes of the clematis, to which persistent hairy styles are attached (Fig. 97, c), and the cypselas of the dandelion and thistle, in which wind-dispersal is facilitated by the hairy calyx, or pappus, which is attached to each cypsel.

A number of capsular fruits contain hairy seeds which are blown away when the fruit dehisces. The capsules of the willow and willow-herb produce numerous small seeds, the testas of which develop local plumose structures.

Some seeds are of flat form and may be blown away on exposure to the wind, as in the case of the stock and the honesty.

In a few cases seeds, without particular specialisation, may be wind-dispersed, as in the orchids, the capsules of which produce large numbers of exceedingly small seeds.

Dispersal by Water.

The seeds of aquatic Angiosperms may be dispersed by water currents, as can the seeds of land plants if they fall into streams and rivers. Few British plants possess seeds specially adapted for water-dispersal, but one example is the water-lily. The seeds of the water-lily have a spongy investment, or *aril*, which contains air-spaces enabling the seeds to float when they are liberated from the capsule in which they are formed. The aril becomes water-logged, or rots, after a time, and the seeds sink to the muddy bed of the pond or stream.

The coco-nut is an example of a sea-borne fruit which may be carried for long distances before it is thrown on to a shore where germination of the seed can occur.

Dispersal by Animals and Birds.

Fruits may be dispersed by animals and birds, and are usually characterised by the possession of hooks, or a succulent coating.

Birds, in particular, are important agents in the dispersal of succulent fruits and false-fruits, which they may carry over long distances in a short time. Fruits dispersed by this means can be

larger than those carried by the wind. Those fruits eaten by birds possess seeds with an indigestible covering which permits them to pass through the digestive tract of the bird without injury. The seeds are deposited with the droppings and can then germinate. The seeds of drupes and drupels are protected by the hard endocarp of the fruit, and those of berries by their hard testas.

Succulent false-fruits, like the strawberry and the hip, may have their achenes dispersed by birds, because of the edible nature of the receptacle.

Animals with furry coats serve to disperse a number of fruits which have pericarps, or other structures, bearing hooks. The achenes of the corn-buttercup have a spiny pericarp, whilst those of the avens have a persistent style, which breaks at the tip to form a hook. The goosegrass fruit has a pericarp covered with small hooked hairs, as has that of the enchanter's nightshade. The cypsela of the bur-marigold has a series of barbed spines, which represent the persistent calyx, and in the agrimony, the receptacle is hooked. The cypselas of the burdock are enclosed in an involucre of hooked bracts, so that if the head of fruits becomes attached to an animal the cypselas will be gradually shed as the animal moves about (Fig. 97, 1).

Birds and other animals may assist in an indirect way in the dispersal of fruits and seeds not specialised for this means of dispersal. This occurs when they walk over sticky soils which may become attached to their feet and pick up various seeds. When the soil cakes and dries it will fall off, together with the seeds.

Explosive Fruits.

A number of dry fruits, when fully ripe, break open violently and throw their seeds to considerable distances.

This occurs in the siliqua of the bitter-cress, the pod of the gorse, and the regma of the cranesbill. In the violet, the capsule splits into three boat-shaped parts, and the sides of each constrict to squeeze out the seeds. The berry of the squirting-cucumber becomes so turgid when ripe that the central pulp, with its contained seeds, is ejected forcibly from one end of the fruit.

Censer Mechanisms.

A censer is a vessel used in ceremonial rites for the scattering of incense. Some capsular fruits open when ripe, but depend on the swaying movements of the plant to scatter the seeds. This type of dispersal is found in the capsule of the poppy, the seeds of which are shed through pores, and the capsule of the campion which opens by apical teeth. A censer mechanism may be involved in the siliqua of the wallflower and similar plants, after the carpels

have broken away leaving the seeds attached to the replum from which they are ultimately shaken.

It may be mentioned, in conclusion, that man has often assisted in seed-dispersal, owing to his movements from place to place, and to the conveyance of merchandise. By this means alien plants have been introduced into regions where no natural means of dispersal would have been effective, because of such natural barriers to the spread of plants as oceans, mountain ranges and deserts.

CHAPTER XVIII

THE CLASSIFICATION OF ANGIOSPERMS

The Angiosperms are divided into two large sub-classes, the Dicotyledons and the Monocotyledons, which differ in several well-marked features.

The Dicotyledons, which are considered to be the older group, are characterised by the presence of a ring of open collateral vascular bundles in their stems, by reticulate venation of their leaves, by the floral parts commonly being arranged in fours or fives and by their seeds having dicotyledonous embryos.

The Monocotyledons have stems with a scattered arrangement of closed collateral bundles, leaves with parallel venation (with few exceptions) flowers with the parts arranged in threes, and seeds with monocotyledonous embryos.

The Dicotyledons include woody as well as herbaceous plants, the stems and roots of the woody forms undergoing secondary growth in thickness, whereas in the Monocotyledons there are no truly woody members, although such types as *Dracæna* have a tree-like habit.

The two sub-classes are divided into a number of families, and the members of each family agree in certain details which are taken to indicate relationship. The characters employed to delimit the various Angiosperm families are largely floral, for whilst there may be great variation between the flowers of different families, when a number of species present the same essential plan of floral structure there is little doubt that they are related and have originated from one ancestral form. Further, the flower is the most conservative part of the plant, for although, during the evolution of Angiosperms, certain variations of floral structure arose, once a particular type of floral architecture was established, it remained relatively stable afterwards.

Vegetative characters are of little value in the classification of plants, for the vegetative organs appear to become modified with comparative ease, so fitting a plant for a particular mode of life.

It has been seen already how the form of the root, stem and leaf may be modified, and the same type of modification can occur in plants that are not closely related. For example, the aquatic

Angiosperms belong to numerous distinct families, yet, because of their mode of life, their vegetative structure is similar. The water crowfoot (*Ranunculus aquatilis*, Fig. 50) which belongs to the family Ranunculaceæ, cannot be readily distinguished, in the vegetative condition, from another aquatic plant, a water celery (*Apium inundatum*, Fig. 50) which is a member of the family Umbelliferae. When the plants are in flower, however, there is no difficulty in identification, as each produces the characteristic flower of its family. In these examples it is found also that, whilst there is a great difference between their vegetative form and that of their terrestrial relatives, there is a close similarity between the flowers of the aquatic and land types of a particular family, which emphasises the constancy of the floral structure.

Vegetative characters may have some importance in the classification of Angiosperms, as has already been suggested in outlining the characters of the Dicotyledons and Monocotyledons. The structure of the vascular bundle amongst the Dicotyledons is sometimes an aid in distinguishing members of different families which may have some floral similarity. For example, the members of the family Solanaceæ possess stems with bicollateral vascular bundles, and thus may be distinguished from certain members of the family Scrophulariaceæ, which they superficially resemble.

In some families the inflorescence is a feature of systematic importance, the capitulum (p. 224) being characteristic of the family Compositæ, and the compound umbel (p. 221) being found only in the family Umbelliferae.

The floral characters which are important in the classification of the Angiosperms include the insertion of the floral whorls on the receptacle, the details of the perianth, the number and arrangement of the stamens and the structure of the pistil. In the systematic description of the flower, certain methods are used as an aid to comparative study. These include the *longitudinal section*, the *floral diagram* and the *floral formula*.

The longitudinal section of the flower is used to indicate the insertion of the floral whorls and the relative levels of the floral parts. The true longitudinal section is represented by a drawing of the exposed edge of the flower when cut longitudinally through its plane of symmetry. In some cases, e.g. the mustard flower, such a drawing is not satisfactory, as one or other of the floral whorls may not occur in the plane of symmetry, so that a drawing of the *half flower* is more suitable, as it not only includes the plane of symmetry, but the internal view of the half flower also.

The floral diagram is a plan of the flower with the whorls projected in such a way as to show their position round the apex of

the receptacle. In a floral diagram, the various whorls are arranged in a concentric series indicating the number of members in each whorl, and their cohesion and adhesion, if they occur. When possible, it is customary to show the position of the axis of the inflorescence and of the bract in the axil of which the flower is borne; the parts of the flower next to the axis are *posterior*, those next to the bract *anterior*.

A method of summarising floral structure is by means of a floral formula, in which certain symbols are used, and the number of parts of each whorl follows the symbol denoting that whorl. When the whorls are coherent, the number is enclosed by a bracket, and when distinct whorls are adherent, a bracket joining them is used. The superior ovary is shown by a horizontal stroke below the symbol for the gynæcium and for an inferior ovary the stroke is placed above.

The symbols used are as follows :

\oplus = Regular	\uparrow = Irregular
σ = Male (Staminate)	♀ = Female (Pistillate)
♂ = Hermaphrodite.	

P = Perianth (when two distinct whorls are not present)

K = Calyx

C = Corolla

A = Andræcium ∞ = Indefinite stamens

G = Gynæcium ∞ = Indefinite carpels

Some examples of floral formulæ are :

Buttercup : K5 C5 A ∞ G ∞

Sweet Pea : K(5) C5 A(9) + 1 G $\underline{1}$

Hogweed : K5 C5 A5 G($\underline{2}$)

Deadly Nightshade : K(5) C(5) A5 G($\underline{2}$)

Tulip : P3 + 3 A3 + 3 G($\underline{3}$)

Dicotyledons

Family *Ranunculaceæ*

This is a widely distributed family, although the majority of the members occur in temperate regions. It consists, for the most part, of perennial herbs with root-tubers, e.g. lesser celandine (*Ranunculus ficaria*, Fig. 16), corms, e.g. bulbous buttercup (*Ranunculus bulbosus*), and rhizomes, e.g. *Anemone*. Several members are woody, but the only British plant of this habit is *Clematis*. Many members have acrid juices and are poisonous, a number which include monkshood (*Aconitum*) being important as drug plants.

The leaves may be simple, as in marsh marigold (*Caltha*), or much divided as in monkshood (Fig. 2, E), and are usually exstipulate and alternately arranged.

The inflorescence varies with different members; in monkshood it is racemose, in buttercup, cymose, and in *Anemone*, a solitary flower is produced.

The flowers are hermaphrodite, hypogynous, have all parts free, and are mostly regular. The perianth may consist either of one petaloid whorl, as in *Anemone*, or of typical calyx and corolla as in buttercup (Fig. 87), or with a petaloid calyx and a modified corolla as in monkshood. The perianth whorls usually consist of five segments. The androecium consists of indefinite stamens, and the pistil is apocarpous. Each carpel may contain a single ovule, e.g. buttercup, or many ovules, e.g. larkspur (*Delphinium*).

The resultant fruit is usually either an etærio of achenes, e.g. buttercup (Fig. 97, A), or an etærio of follicles, e.g. larkspur (Fig. 98, A), but in love-in-a-mist (*Nigella*), a capsule is formed, and in baneberry (*Actæa*), the fruit is a berry.

The flowers are insect-pollinated, and generally possess nectaries. The nectaries of buttercup are on the bases of the petals (Fig. 87), those of monkshood represent modified petals (Fig. 103, B), whilst in marsh marigold they occur on the receptacle at the base of the carpels.

The Genera include :

Ranunculus.

This is a large genus which includes :

R. acris (meadow buttercup, Fig. 87). Flower, regular with five green sepals, five yellow petals, on the bases of which are small scale-like nectaries, indefinite stamens and carpels.

R. repens (creeping buttercup). Reproduces itself vegetatively by runners.

R. aquatilis (water crowfoot, Fig. 50). An aquatic species with floating and submerged leaves.

Floral Formula : $K5 C5 A\infty G\underline{\infty}$.

Anemone nemorosa (wood anemone). A single regular flower borne on solitary aerial stem, which has an involucre of bracteoles. Perianth of six free petaloid sepals, corolla absent. No nectar, visited by insects for pollen. Fruit, an etærio of achenes.

Floral formula : $K6 C0 A\infty G\underline{\infty}$.

Clematis (traveller's joy). A woody climber of hedgerows and woods with opposite, pinnately compound leaves, climbing by means of sensitive petioles (Fig. 18, B). Regular flower with calyx

of four greenish-white sepals, corolla absent. A pollen flower. Fruit, an etærio of achenes, the styles usually persisting as plumose structures which aid dispersal of fruits (Fig. 97, c). There are several cultivated species with conspicuous, coloured sepals.

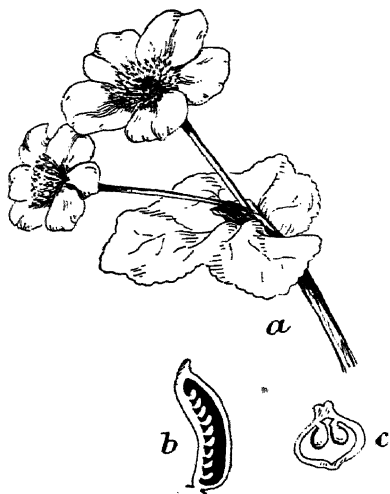


FIG. 102.—Marsh Marigold (*Caltha palustris*).

a, flowering shoot ($\times \frac{1}{2}$); *b*, longitudinal section of carpel ($\times 2$); *c*, transverse section of carpel, showing marginal placentation ($\times 4$).

petals, in which nectar is secreted, indefinite stamens and pistil of five free carpels. Fruit, an etærio of follicles.

Floral formula : $K5 C5 A\infty G\bar{5}$.

Delphinium ajacis (larkspur, Fig. 103, D–F). Occurs wild occasionally, but is cultivated as an ornamental garden plant. Flower, zygomorphic, with petaloid calyx of five sepals, the posterior sepal being projected backwards as a spur; coloured corolla represented by four modified petals, two of which form nectaries which project into the spurred sepal; indefinite stamens, and pistil of one to five carpels. Fruit, an etærio of follicles.

Floral formula : $K5 C4 A\infty G1-5$.

Aconitum napellus (monkshood, Fig. 103, A–C). A tall plant of shady places, now cultivated as an ornamental plant and for its medicinal use. Flower, zygomorphic, with petaloid calyx of five purple sepals, the posterior sepal forming a hood, protecting two posterior petals which are modified to form green, hooked nectaries,

Thalictrum (meadow rue). Stipulate leaves. Small apetalous flowers with prominent anthers.

Caltha palustris (marsh marigold, Fig. 102). Grows in swampy places. Regular flower with petaloid calyx; no corolla. Fruit, an etærio of follicles.

Helleborus niger (Christmas rose). Petaloid, greenish-white sepals; petals modified into tubular nectaries. Fruit, an etærio of follicles.

Helleborus viridis (Hellebore).

Aquilegia vulgaris (Columbine).

Occurs wild in certain parts of Britain, but is cultivated as an ornamental plant. Flower regular with calyx of five petaloid sepals, corolla of five coloured, spurred

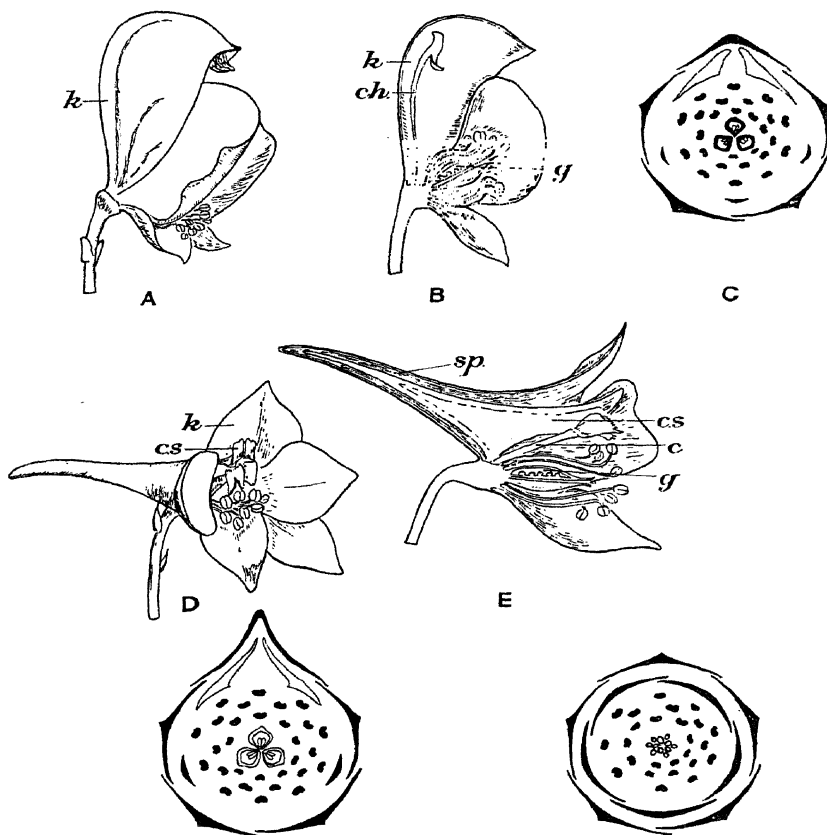


FIG. 103.

A, Monkshood (*Aconitum*), flower ($\times \frac{3}{4}$); B, half-flower; C, floral diagram; D, Larkspur (*Delphinium*), flower ($\times \frac{3}{4}$); E, half-flower; F, floral diagram; G, floral diagram of Buttercup (*Ranunculus*).

(c = modified petal, ch. = petal modified to hooked nectary, c.s. = petal modified to spurred nectary, g = carpel, k = petaloid calyx, sp. = spurred sepal.)

whilst the other petals may be reduced or suppressed; indefinite free stamens, and a pistil of three to five carpels. Fruit, an etærio of follicles.

Floral formula: $K5 C5 A\infty$

Family *Leguminosæ*

This is a large family of wide distribution in tropical and temperate regions, and consists of members showing variation in

vegetative habit and in floral structure. The family is divided into three sub-families, Mimosoideæ, Cæsalpinioideæ and Papilionatæ, the last, including all the British genera. It is of economic importance, as it includes ornamental species, e.g. sweet pea (*Lathyrus odoratus*) and laburnum (*Cytisus*), food plants, e.g. bean (*Vicia*) and pea (*Pisum*), forage plants, e.g. clover (*Trifolium*) and vetch (*Vicia*), and drug plants which yield liquorice, senna and tragacanth. Some members of the family are poisonous, including lupin (*Lupinus*) and certain species of *Astragalus*.

The family consists of annual and perennial herbs, shrubs and trees, several of the members showing a climbing habit. The roots usually possess nodules, small swellings infected with a nitrogen-fixing bacterium (p. 100). The stipulate leaves are generally alternately arranged and pinnately compound, and the terminal leaflets often modified into tendrils for climbing purposes.

The racemose inflorescence consists of hermaphrodite, perigynous flowers, with monocarpellary pistils. The characteristic fruit is a legume, though occasionally a lomentum is formed.

Sub-family. *Mimosoideæ*

This consists of tropical and sub-tropical genera which include *Acacia* (Fig. 104), species of which yield gum arabic, and *Mimosa*,



FIG. 104.—*Acacia*.

a, shoot with inflorescences ($\times \frac{1}{2}$); *b*, inflorescences ($\times 1$); *c*, section of one inflorescence ($\times 3$); *d*, half-flower ($\times 6$).

which includes the sensitive plant, *Mimosa pudica* (Fig. 60). The flowers are small and regular with free stamens, either indefinite as in *Acacia*, or equal in number to the perianth segments as in *Mimosa*.

Floral Formulæ :

<i>Acacia</i> . . .	K(4) C4 A ∞ G1
<i>Mimosa</i> . . .	K(4)-(5) C4-5 A4-5 or 2(4-5) G1

Sub-family. *Cæsalpinioideæ*

There is much variety of floral structure in this sub-family, the genera of which are intermediate in type between Mimosoideæ and Papilionatæ. The flowers are mostly irregular, with a calyx of five sepals, corolla of five petals, androecium of ten stamens, which are generally free, though some may be sterile, taking the form of staminodes.

The Genera include :

Cassia. Leaflets (Fig. 2, F) and fruits of some species yield senna leaf and pod.

Hæmatoxylon. The heart wood of the stem is the logwood of commerce and yields the purple dye, hæmatoxylin.

Tamarindus. Produces a succulent, edible pod.

Bauhinia. A woody climber of tropical forests with stipular tendrils.

Cercis. An ornamental tree.

Sub-family. *Papilionatæ*

This includes a number of herbaceous and woody plants.

The flower is irregular, due to the specialised nature of the corolla. The calyx consists of five united sepals, and may in some cases have a bilabiate structure. The corolla of five petals is described as *papilionaceous*, and is composed of a large posterior petal, the *vexillum*, which overlaps the other petals in the bud, viz. two lateral petals or *alæ*, and two anterior petals which cohere by their lower margins to form the *carina*. The last encloses the essential organs which consist of ten stamens, either monadelphous or diadelphous, and a pistil of one carpel with a long, superior ovary having marginal placentation, a curved style and a hairy stigma. In the flower with a diadelphous androecium a nectary is situated at the base of the ovary, and the movable, posterior, free stamen facilitates the obtaining of the nectar by pollinating insects such as bees.

Floral Formulæ :

Sweet pea	K(5) C5 A(9) + 1 G1
Orchard	K(5) C5 A(10) G1

The Genera include :

Lathyrus odoratus (sweet pea, Fig. 105). An ornamental climbing plant with leaflet tendrils (Fig. 18, A). Diadelphous andrœcium.

Lathyrus Aphaca (yellow vetchling). No leaflets, but unbranched leaf tendril and large stipules (Fig. 18, c).

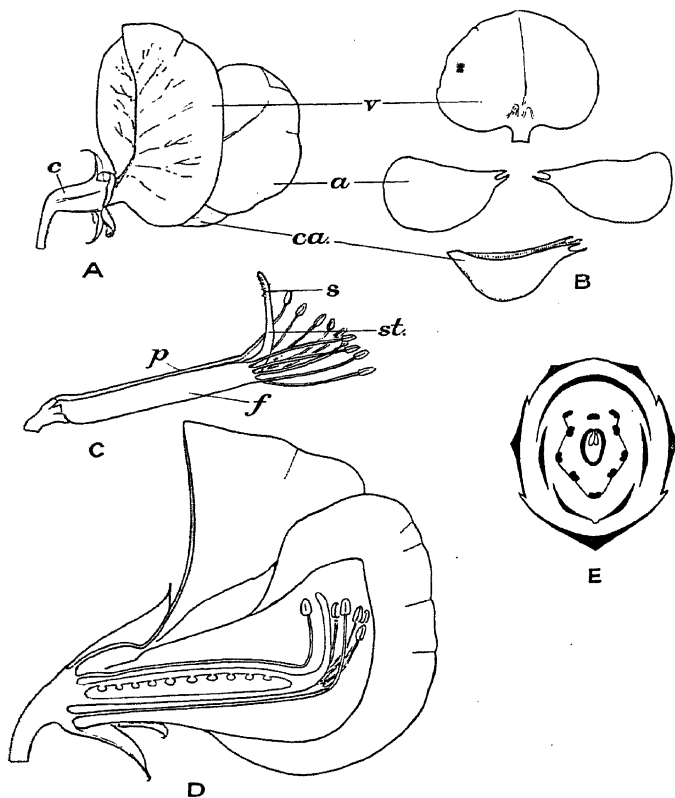


FIG. 105.—Sweet Pea (*Lathyrus*).

A, flower ($\times \frac{1}{2}$); B, parts of corolla; C, essential organs ($\times 1$); D, half-flower ($\times 1$); E, floral diagram.

(a = ala, c = calyx, ca. = carina, f = fused filaments of 9 stamens, p = free posterior stamen, s = stigma, st. = style, v = vexillum.)

Vicia sativa (vetch). Occurs wild and also cultivated for forage. Climbs by leaflet tendrils. Diadelphous andrœcium.

Vicia faba (broad bean).

Phaseolus (scarlet runner, kidney bean). A climbing plant with twining stem.

Trifolium (clover). A common plant of pastures with small flowers compactly arranged in a compact spike. Diadelphous andrœcium.

Medicago (medick). Cultivated as a forage plant. Legume spirally coiled, and usually spiny and indehiscent.

Lotus (bird's-foot trefoil).

Ulex europæus (gorse, Fig. 106). Occurs on dry soils. Leaves and axillary branches modified into green spines. Calyx consists of upper and lower parts representing two and three sepals respectively. Monadelphous andrœcium. Explosive legume.

Cytisus (broom, laburnum). Small compound leaves. Monadelphous stamens.

Genista. Simple leaves.

Robinia (false acacia). Compound leaves with stipular spines.

Onobrychis (sainfoin), *Ornithopus*

(bird's-foot), *Hippocrepis* (horseshoe vetch); fruit, a lomentum.

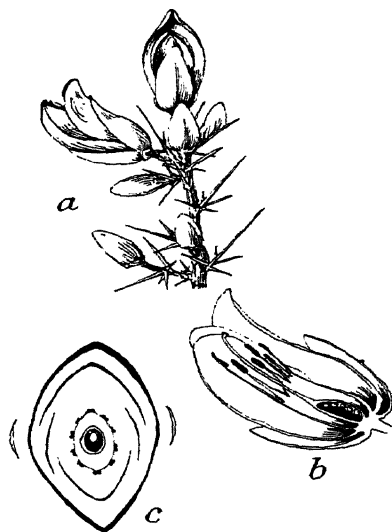


FIG. 106.—Gorse (*Ulex europæus*).

a, flowering shoot ($\times \frac{3}{8}$); *b*, half-flower ($\times 1\frac{1}{2}$); *c*, floral diagram—note monadelphous andrœcium and two-partite calyx.

Family *Umbelliferae*

This is a large family of herbaceous plants most of which are perennials, e.g. hogweed (*Heracleum*), although annuals, e.g. coriander (*Coriandrum sativum*, Fig. 107) and biennials, e.g. hemlock (*Conium maculatum*) and carrot (*Daucus carota*, Fig. 107) also occur.

The family is important economically as it contains a number of aromatic plants which yield oil, including fennel (*Foeniculum vulgare*), anise (*Pimpinella anisum*), caraway (*Carum Carvi*) and coriander; food plants such as carrot, celery (*Apium*), parsnip (*Peucedanum sativum*) and parsley (*Carum Petroselinum*), and poisonous plants such as hemlock and water dropwort (*Enanthe crocata*).

The vegetative and floral characters are very uniform throughout the family, the aerial shoots possessing ridged stems with hollow internodes, and alternately-arranged, exstipulate, compound leaves with sheathing leaf-bases (Fig. 108, *A*).

The small flowers are usually arranged in compound umbels

(Fig. 108, A) although several members including marsh pennywort (*Hydrocotyle*) have solitary flowers, and in sea holly (*Eryngium maritimum*), a head of sessile flowers is produced. At the base of the compound umbel an involucre of bracts usually occurs, and at the base of each umbel, an involucre.

The flowers are hermaphrodite, epigynous, and regular except for a slight zygomorphy in the petals of the flowers on the outer margin of the inflorescence. The calyx is minute, and in some cases is represented only by a narrow, circular ridge; the corolla of five free petals is usually white, yellow or pink in colour and the tips often turned in or inflexed; the five free stamens alternate with the

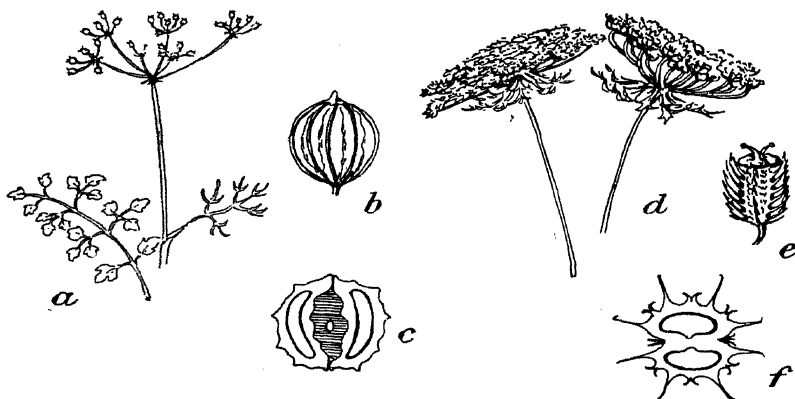


FIG. 107.—Coriander (*Coriandrum sativum*).

a, inflorescence and leaves ($\times \frac{1}{2}$); *b*, cremocarp ($\times 3$); *c*, transverse section of cremocarp. Carrot (*Daucus carota*). *d*, inflorescences ($\times \frac{1}{2}$); *e*, spiny cremocarp ($\times 2$); *f*, transverse section of cremocarp.

petals, and the pistil consists of two united carpels. The inferior ovary is bilocular, each loculus containing a single, pendulous ovule, and the upper surface of the ovary is occupied by a swollen disc-like nectary continuing into the two styles which terminate in spherical stigmas. The characteristic fruit is a cremocarp (p. 202). The seed possesses a small embryo embedded in an oily endosperm.

The flowers, which are usually protandrous, are pollinated by short tongued insects, such as flies, the nectar being easily accessible.

Floral formula : $K_5 C_5 A_5 \overline{G(2)}$.

The Genera include :

Heracleum (hogweed, Fig. 108). A common weed with conspicuous inflorescences and flattened cremocarps.

Astrantia. A cultivated plant occasionally found wild, in which

the involucrel bracts are fused and conspicuous and completely surround the flowers within.

Conopodium (earthnut). Produces tuberous, edible rhizome.

Myrrhis odorata (sweet Cicely). Fruit (Fig. 99, κ).

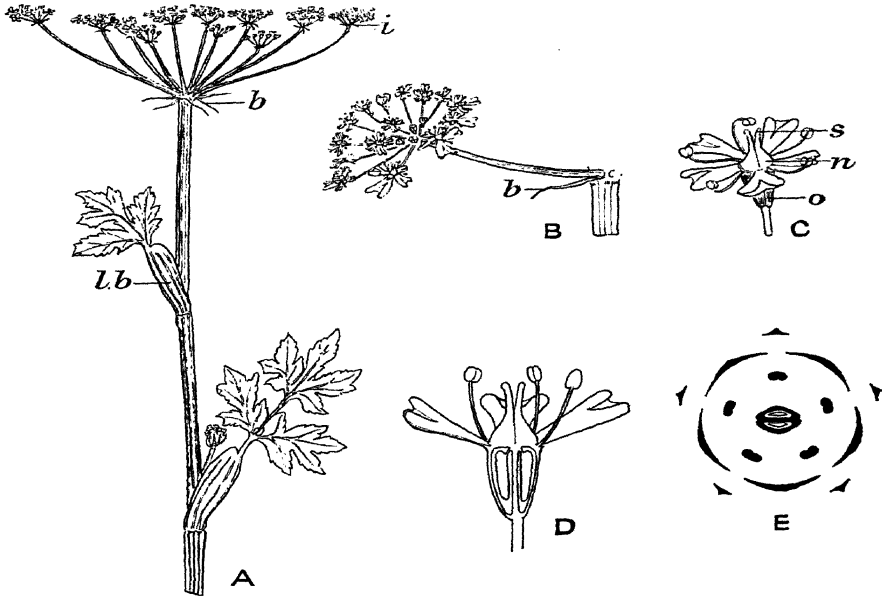


FIG. 108.—Hogweed (*Heracleum*).

A, flowering shoot ($\times \frac{1}{2}$); B, partial inflorescence (umbel) ($\times 1\frac{1}{2}$); C, single flower ($\times 3$); D, half-flower ($\times 5$); E, floral diagram.

(b = involucrel bract, i = involucrel, lb. = leaf-base, n = nectary, o = ovary, s = stigma.)

Chærophyllum (chervil).

Crithmum maritimum (samphire). Grows in exposed places near the sea and has fleshy leaves and stems, a common feature of halophytes (p. 89).

Angelica, preserved stem used in confectionery.

Family *Solanaceæ*

The members of this family are widely distributed in tropical and sub-tropical regions, but several, including woody nightshade or bittersweet (*Solanum Dulcamara*), and deadly nightshade (*Atropa Belladonna*) are found wild in Britain.

The family is of economic importance, for not only does it include the potato (*Solanum tuberosum*), the tomato (*Lycopersicum escu-*

lentum) and the red peppers (*Capsicum spp.*), but its members are rich in alkaloids, some of which are used medicinally. On account of the presence of alkaloids many members are poisonous in some degree, the more potent forms including deadly nightshade, henbane (*Hyoscyamus niger*) and thorn apple (*Datura Stramonium*). Tobacco consists of the dried leaves of *Nicotiana Tabacum* containing the alkaloid nicotine. The temperate members are mostly herbaceous; tropical forms may be shrubs or trees. The potato and several of its relatives are characterised by the development of stem tubers, whilst the deadly nightshade perennates by its swollen tap root. The stems possess bicollateral vascular bundles, and the leaves are usually simple, exstipulate and alternately arranged.

The flowers, solitary or arranged in cymes, are hermaphrodite, hypogynous and generally regular.

The gamosepalous calyx consists of five sepals, usually persistent; the sympetalous corolla of five petals has a variety of form in different members and bears five epipetalous stamens; the syncarpous pistil of two carpels has a superior bilocular ovary with axile placentation, and a nectary occurs at the base of the ovary. The fruit may be either a capsule or a berry.

Floral Formula : $K(5) \overline{C(5)} A5 \underline{G(2)}$.

The Genera include :

Atropa Belladonna (deadly nightshade, Fig. 109, A-C). Occurs wild on the more calcareous soils of Britain, and now cultivated extensively on account of its medicinal value. Perennial herb with erect stem, smooth ovate leaves (Fig. 2, A) and solitary, pendulous flowers. Corolla, purple and campanulate. Fruit, a dark purple berry subtended by spreading calyx. Atropine and other alkaloids obtained from root and leaf.

Solanum Dulcamara (woody nightshade, Fig. 109, D). Woody climber of hedgerows, climbing by sensitive petioles. Corolla of purple petals fused at their bases to form a shallow tube. Stamens with prominent anthers dehiscing apically and cohering to form a tube around the style. Fruit, an oval red berry.

Hyoscyamus niger (henbane). Annual or biennial herb, now cultivated for drug purposes. Corolla, yellowish in colour, often faintly veined with purple and with five unequal teeth. Fruit, a bilocular capsule enclosed by calyx and dehiscing by a lid (Fig. 98, M).

Datura Stramonium (thorn apple). Introduced into Britain as a cultivated form but has occasionally escaped and occurs as a casual annual weed. Cultivated for its medicinal use. Stems, erect and smooth; leaves, large, ovate and smooth. Corolla, large, funnel-

shaped and usually white. Fruit, a spiny capsule dehiscing by four valves.

Physalis (winter cherry). Fruit, a berry enclosed by a coloured, inflated calyx.

Schizanthus. An ornamental greenhouse plant. Corolla, irregular; stamens, two fertile, others represented by staminodes (sterile stamens).

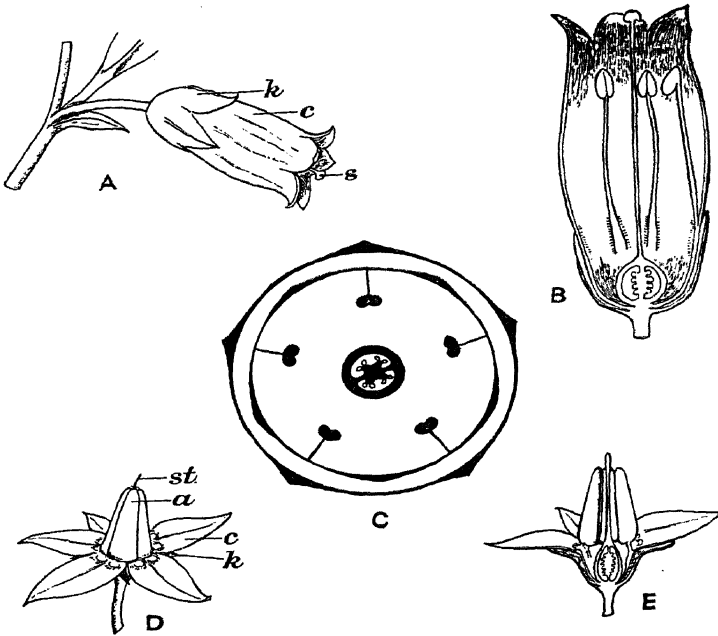


FIG. 109.

A, flower of Deadly Nightshade (*Atropa*) ($\times \frac{1}{2}$); B, half-flower ($\times 1$); C, floral diagram; D, flower of Bittersweet (*Solanum*) ($\times 1$); E, half-flower ($\times 1$).
(a = anther, c = corolla, k = calyx, s = stigma, st. = style.)

Family *Compositæ*

This is the largest family of Angiosperms, its genera being widely distributed in all parts of the world. This is probably due to the compact inflorescences which facilitate cross-pollination, and to the efficient means of fruit-dispersal possessed by many of its members. Annual and perennial herbs, shrubs and trees are found in the family, though all the British genera are herbaceous.

Inulin is a common food-reserve, being found, for example, in the swollen tap root of dandelion (*Taraxacum*), in the root-tubers

of *Dahlia* and in the stem-tubers of Jerusalem artichoke (*Helianthus tuberosum*)

The family includes food plants such as the artichokes (*Helianthus Cynara Scolymus*), lettuces (*Lactuca*), and chicory (*Cichorium*), drug plants such as chamomile (*Matricaria*) and *Pyrethrum*, and ornamental plants such as *Chrysanthemum*, *Dahlia* and other well-known genera. Many members are weeds of cultivated land and include thistles (*Carduus*), groundsel (*Senecio vulgaris*) and ragwort (*Senecio Jacobæa*).

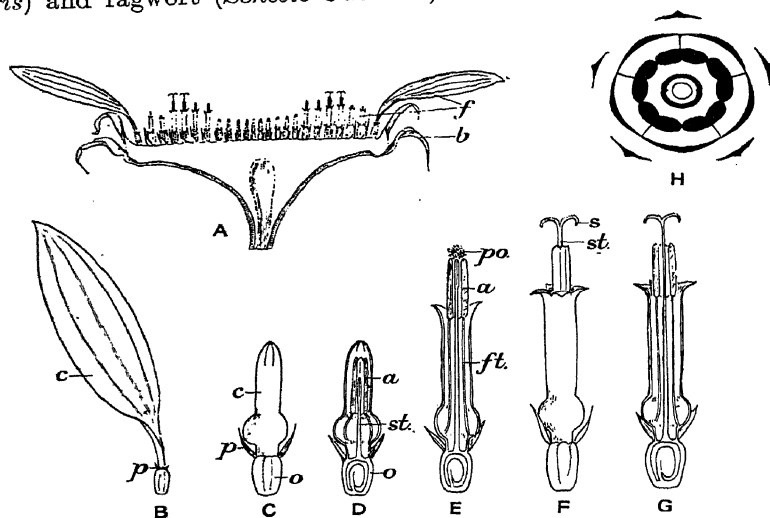


FIG. 110.—Sunflower (*Helianthus*).

A, L.S. of capitulum ($\times \frac{1}{4}$); B, sterile ray-floret ($\times \frac{1}{2}$); C-G, stages in development of disc-floret ($\times 3$) (D, E and G, sectional view); H, floral diagram.

(a = anther, b = involucre bract, c = corolla, f = florets, ft. = filament, o = ovary, p = calyx, po. = pollen, s = stigma, st. = style.)

The exstipulate leaves are generally simple, and may be alternately or oppositely arranged. The racemose inflorescence, a capitulum (Fig. 86, D; 110, A) is characteristic and consists of a flattened axis bearing numerous small flowers or florets, surrounded by whorls of bracts forming an involucre.

The flowers are epigynous and pentamerous, and may be hermaphrodite, unisexual or sterile, and regular or irregular. The calyx is invariably modified and frequently assists in fruit-dispersal. The corolla consists of five fused petals, forming either a ligulate corolla with five small teeth as in dandelion, or a regular tubular corolla as in groundsel, or an irregular tubular corolla of

a bilabiate form as in cornflower (*Centaurea*). The five stamens are epipetalous and syngenesious, and the pistil is composed of two united carpels with an inferior ovary containing a single erect ovule, a long style and a bilobed stigma. The fruit is a cypsela, to which the modified calyx may remain attached. In dandelion and thistle, the calyx persists as a whorl of hairs or pappus (Fig. 97, g) assisting wind-dispersal, whilst in bur marigold (*Bidens cernua*), the calyx consists of barbed bristles which enable animal-dispersal to take place. In burdock (*Arctium*, Fig. 97, l), the cypselas have no specialisation for dispersal, but the involucre bracts are hooked, so that the whole capitulum may be carried away in the coat of an animal, the fruits being shed as the animal moves about.

Nectar occurs at the base of the style, the flowers being insect-pollinated and generally protandrous (p. 194). The florets of a capitulum mature from without inwards, so that cross-pollination may occur between the outer, older florets and the inner, younger florets as insects pass across the inflorescence.

The composition of a capitulum shows variation with regard to its component florets.

The family is divided into two sub-families, Tubulifloræ and Ligulifloræ. In Tubulifloræ the tissues of the vegetative organs do not contain a milky fluid, latex, and either all or some of the florets have tubular corollas. In many members the outer part of the capitulum is composed of conspicuous, ligulate *ray florets* which surround a central region of tubular *disc florets* (Fig. 110). In Ligulifloræ, the tissues contain latex, and all the florets have ligulate corollas.

Floral Formula of a typical hermaphrodite floret, e.g. dandelion :

Sub-family *Tubulifloræ*

The Genera include :

Helianthus annuus (sunflower, Fig. 110). A cultivated plant with opposite leaves and attractive capitula. Capitulum consists of sterile, ligulate ray florets and hermaphrodite tubular disc florets. Calyx modified to scales. Cypsela without pappus.

Bellis perennis (daisy). A rosette plant reproduced vegetatively by runners. Capitulum with pistillate, ligulate ray florets and hermaphrodite, tubular disc florets.

Senecio. A large genus, many species of which are common weeds, e.g. *S. vulgaris* (groundsel) which has a capitulum with hermaphrodite, tubular florets and is self-pollinated.

Centaurea (knapweed, cornflower, Fig. 111, D). A genus of many species some of which are cultivated. Capitulum, with involucre of rough bracts, consists of sterile, tubular ray florets and hermaphrodite, tubular disc florets.

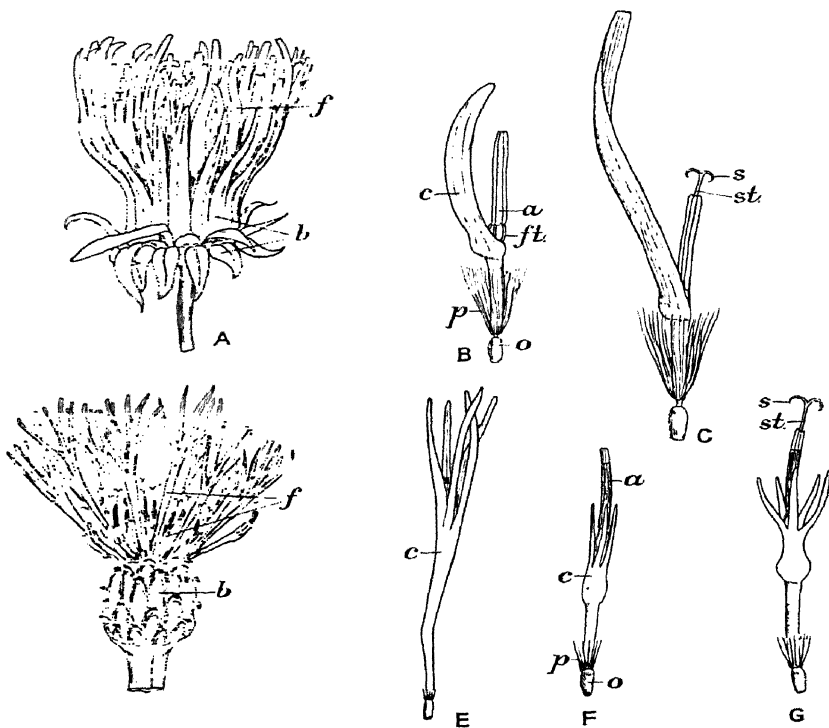


FIG. 111.

A, Dandelion, capitulum; B, young floret; C, older floret; D, Cornflower, capitulum; E, sterile ray-floret; F, young disc-floret; G, older disc-floret.

[A, D $\times 1$, remainder enlarged.]

(a = anther, b = involucre bracts, c = corolla, f = florets, ft. = filament, o = ovary, p = modified calyx, s = stigma, st. = style.)

Tussilago (coltsfoot). Produces florets before leaves in early spring. Capitulum with pistillate, ligulate florets and staminate tubular florets.

Petasites vulgaris (butterbur). Perennial rhizomatous plant growing in moist places. Capitulate racemes with capitula mainly composed of florets of one sex.

Sub-family *Ligulifloræ*

The Genera include:

Taraxacum (dandelion, Fig. 111, A). A common weed of cultivation. Capitulum of hermaphrodite, ligulate florets. Cypsela with stalked pappus.

Tragopogon (goat's beard). A meadow plant with long, narrow leaves encircling the stem. Capitulum and cypsela similar to those of dandelion.

Sonchus (sow-thistle). A weed of cultivation. Capitulum similar to that of dandelion. Cypsela with sessile pappus.

Cichorium (chicory). Perennial herb with capitulum of blue florets.

Monocotyledons

Family *Liliaceæ*

The members of this large family are widely distributed and include a number of ornamental plants such as lily (*Lilium*) and hyacinth (*Hyacinthus*), and several food plants such as onion (*Allium*) and *Asparagus*. The family, in common with the majority of Monocotyledons, consists chiefly of perennial herbs,

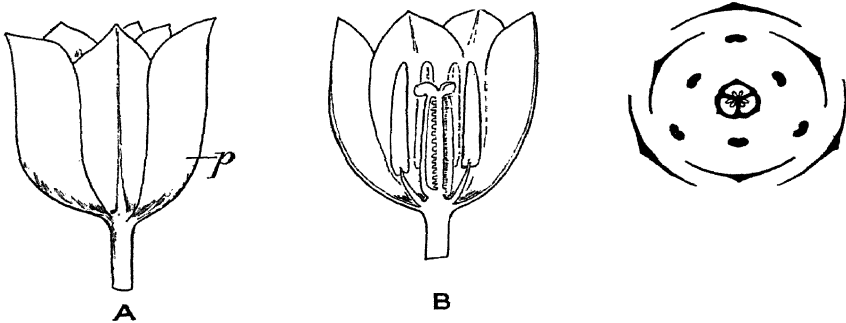


FIG. 112.—Tulip.

A, flower ($\times \frac{1}{2}$); B, half-flower ($\times \frac{1}{2}$); C, floral diagram.

(p = perianth.)

but butcher's broom (*Ruscus*) is a British shrub, and *Dracæna* is a tropical arborescent form.

Perennation is effected by means of bulbs in hyacinth and tulip (*Tulipa*, Fig. 14, A), rhizomes, in lily of the valley (*Convallaria*) and Solomon's seal (*Polygonatum*, Fig. 11, A), and a corm in autumn crocus (*Colchicum*). The aerial vegetative shoot frequently consists of a number of radical leaves with parallel venation, arising

from the subterranean stem. The floral arrangement varies, solitary flowers occurring in tulip, a raceme in lily of the valley, and an umbel in onion.

The flower is characteristically hermaphrodite, regular, hypogynous and trimerous. It consists of a petaloid perianth of two whorls of three segments, free, as in tulip (Fig. 112) or fused, as in lily of the valley; an androecium of six stamens, free, as in tulip, or epiphyllous as in lily of the valley, and a syncarpous pistil of three carpels with a superior, trilocular ovary having axile placentation.

Nectaries occur in the ovary-wall or at the base of the perianth.

The fruit may be either a capsule, as in tulip, or a berry, as in lily of the valley.

Lily of the Valley . . . $\overbrace{P(3+3)} \overbrace{A3+3} \underline{G(3)}$

The Genera include :

Allium. A large genus with several cultivated species having a characteristic odour and including onion, shallot, leek, garlic.

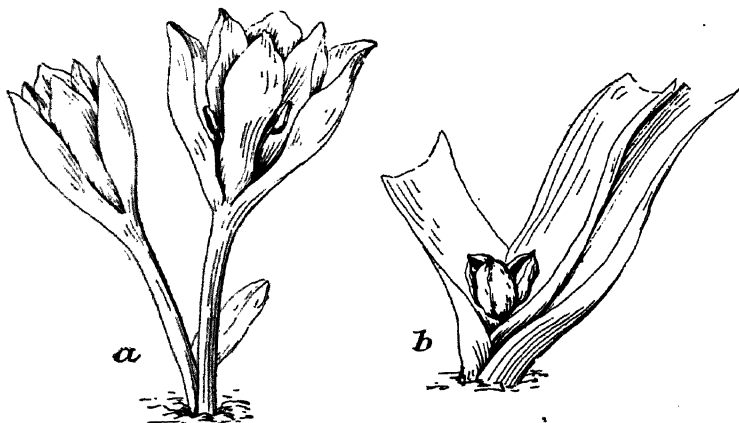


FIG. 113.—Meadow Saffron (*Colchicum autumnale*).

a, autumn condition, with perianth of flower above ground ($\times \frac{1}{2}$); *b*, spring condition, with leaves and fruit (formed by flower of previous autumn) ($\times \frac{1}{2}$).

Perennate by bulbs and possess hollow, tubular leaves. Inflorescence an umbel, bulbils (Fig. 16, c) occasionally replacing flowers. Fruit, a capsule. *Allium ursinum* (ramsons) leaves thin and flat.

Colchicum (autumn crocus or meadow saffron, Fig. 113).

Fritillaria. Some cultivated species. Erect aerial stem bearing leaves, and flowers with campanulate perianth of free segments. Fruit, a capsule.

Lilium (lily). Many cultivated species. Fruit, a capsule.

Scilla nutans (wild hyacinth or bluebell). A common spring flowering plant of shady places. Fruit, a capsule.

Urginea (squill). Bulb is of medicinal use.

Ruscus (butcher's broom). An evergreen shrub. Aerial shoots with small scale leaves producing ovate axillary cladodes (Fig. 19, F), on the upper surfaces of which are small unisexual flowers. Perianth of six, free white segments. Male flower has three stamens and a sterile pistil, female flower has a pistil of three united carpels and three staminodes. Fruit, a red berry.

Asparagus. Immature, etiolated aerial shoots are edible. Mature stem bears thin green cladodes. Fruit, a berry.

Smilax (sarsaparilla). Elongated stem bears net veined leaves and climbs by means of leaf-base tendrils. Root of medicinal value. Fruit, a berry.

Paris quadrifolia (Herb Paris). Occurs in woods in Britain. The rhizome produces, each spring, an aerial stem with a whorl of four net veined leaves and a solitary tetramerous flower. Fruit, a black berry.

Floral Formula : $P_4 + 4 A_4 + 4 \underline{G(4)}$

CHAPTER XIX

INTRODUCTION TO THE ANIMAL KINGDOM. THE COMMON FROG

The frogs are members of a large division of the Animal Kingdom called the Vertebrata, which includes, also, such animals as the fishes, snakes, birds, rabbits and man.

The members of the Vertebrata are characterised by the possession of an internal skeleton, an important part of which is the 'backbone,' or vertebral column, composed of a number of segments, or *vertebræ*. In this character, the vertebrate animals differ from the other members of the Animal Kingdom, which are referred to, collectively, as the Invertebrata.

The vertebrate body is differentiated into *head*, *trunk* and *limbs*, and is *bilaterally symmetrical*, which means that it can be divided into similar halves only in the median plane. Bilateral symmetry involves the distinction between *dorsal* (= upper) and *ventral* (= lower) surfaces, and, owing to the specialisation of the animal, the *anterior* (= front) end of the body is distinguished from the *posterior* (= hinder) end.

The Vertebrata is subdivided into a number of classes, and that to which the frogs, and their relatives, the toads and the newts, are referred is the Amphibia. Amphibians are distinguished by a smooth skin, devoid of hairs or scales, and by the fact that their early life is completely aquatic, but when adult they can live on dry land, having acquired lungs for respiration under such conditions.

The Common Frog (*Rana temporaria*)

The common frog is found in damp situations in Britain where it lives a retiring existence, part of which is spent in water. During the winter it *hibernates* either in the soil, amongst mosses and other damp vegetation, or in the mud at the bottom of a pond or ditch. In the spring it becomes active and migrates to fresh water for the process of spawning, or egg-laying.

The spawn, which consists of a mass of small black eggs protected in a gelatinous slimy coating, is deposited in the water, where, in due course, the eggs hatch to produce the familiar tadpoles. The

tadpole is, at first, a gill-breathing animal without limbs, but by a gradual *metamorphosis*, extending over several weeks, it becomes a frog, which, though small, is typical. Several years elapse before the frog reaches maturity, but in the meantime it spends its life partly on land.

The adult frog is a carnivorous animal, feeding on small insects, grubs, snails, slugs and worms, which it captures either with its jaws, or by means of its specialised tongue.

The frog, especially when in the tadpole stage, is itself preyed on by a number of other animals including water-birds, snakes, fish and aquatic insects.

External Features (Fig. 114).

The frog's body consists of a flat head and trunk, with anterior and posterior pairs of limbs so arranged as to produce the squatting posture which the animal assumes when at rest.

The entire body is covered externally with a slimy skin, of greenish colour above, but light yellow below. The upper skin bears dark spots, which may become more prominent under such external con-

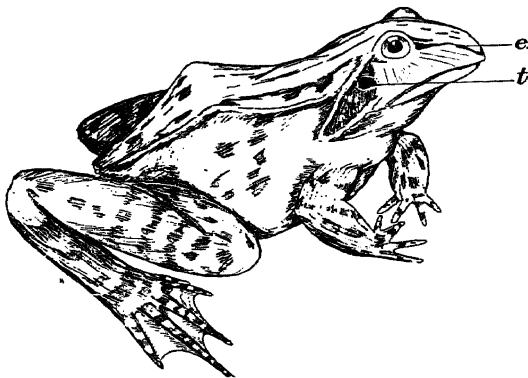


FIG. 114.—Frog (*Rana temporaria*). External Features ($\times \frac{3}{2}$).

(*e.n.* = external nare, *t* = tympanic membrane.)

ditions as cold and darkness, but are less conspicuous under conditions of light and warmth.

The head possesses a large mouth, and placed anteriorly above the nose is a pair of small apertures, the *external nares*, or *nostrils*. The eyes, situated on each side of the head, are protected by *lids*, the upper of which is thick and pigmented, whilst the lower is thin, semi-transparent and freely movable across the eyeball when it is retracted. Immediately behind each eye is a black patch in which is a circular area of skin, the *tympanic membrane*, which indicates

the position of the ear, for the frog has no external ear such as occurs in the rabbit.

The trunk possesses neither neck nor tail, and is of a soft nature, owing to the absence of ribs within. At the hinder end of the trunk and slightly dorsal in position, is the *cloacal aperture*, concerned with the voiding of waste matter, and with the reproductive process.

The skin of the trunk is loosely attached to the underlying body-wall, so that a number of spaces, the *subcutaneous lymph-sacs*, are formed. These lymph-sacs contain a watery fluid, the *lymph*, and water may diffuse through the skin into them from outside.

The limbs have a general structure similar to that of man. The *fore-limbs*, or arms, consist of upper-arm, fore-arm and hand, and the *hind-limbs*, or legs, consist of thigh, leg, elongated ankle and foot. The hand possesses four *digits*, or fingers, and in the male, a fifth digit, or thumb, is indicated by a small swelling which becomes more prominent in the breeding season. The foot has five long toes which are joined together by a covering of skin, forming a *web*. The strong hind-limbs are used for swimming when the animal is in water, and for jumping when on land.

General Internal Anatomy (Fig. 115).

The body-wall is composed mainly of muscular tissue, and, like that of vertebrates in general, is thicker dorsally.

The muscles are attached to the bones of the *skeleton* which is the supporting and protective system of the body, and is called an *endoskeleton* because it occurs within the body.

The skeleton is mainly composed of bony tissue, but part of it is cartilage, which is the only supporting tissue of the tadpole's body, being largely replaced by bone during metamorphosis.

The *skull*, or skeleton of the head, includes the *cranium*, which protects the brain, the *olfactory* and *auditory* or *otic* capsules, protecting the organs of smell and hearing respectively, and the *jaws*, which support the mouth. The *vertebral column* lies in a median position in the dorsal wall of the trunk, and consists of nine small vertebræ, and a posterior elongated *urostyle*. The vertebræ articulate with one another, in order to permit of body movement, and the anterior end of the first, or *atlas vertebra*, articulates with the hinder end of the skull, and allows head movement to occur.

The limb skeleton is associated with two skeletal structures in the trunk, viz. the *pectoral*, or *chest girdle*, and the *pelvic* or *hip girdle*. The pectoral girdle is more or less semicircular, its ventral part forming the 'breast-bone,' or *sternum*, whilst the shoulders are supported by *clavicle*, *coracoid* and *scapula*. The pelvic girdle is V-shaped, and of stronger nature than the pectoral girdle as it has to bear the stresses applied to it when the animal uses its

strong hind-limbs. Each limb is supported by a number of bones, so associated as to allow the movement of the various parts of the limb. There is little difference between the skeleton of fore- and

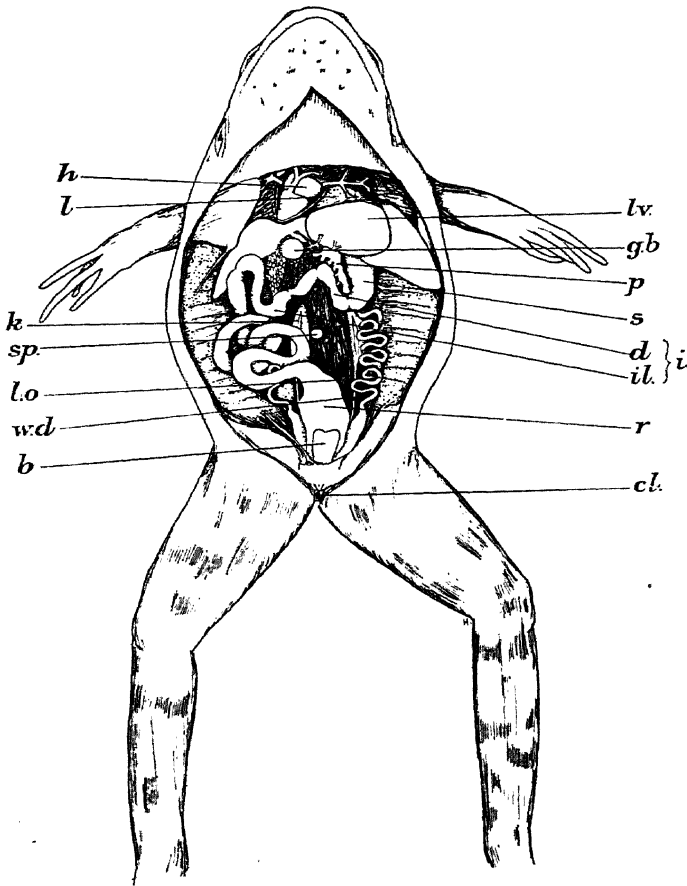


FIG. 115.—Frog. General Dissection of Female (Ventral View).

(*b* = urinary bladder, *cl*. = cloacal aperture, *d* = duodenum, *g.b.* = gall-bladder, *h* = heart, *i* = small intestine, *il.* = ileum, *k* = kidney, *l* = lung, *l.o.* = left oviduct, *lv.* = liver, *p* = pancreas, *r* = rectum, *s* = stomach, *sp.* = spleen, *w.d.* = Wolffian duct.)

hind-limbs, and both are very similar to that found in other vertebrates, which suggests the origin of the various types of vertebrate limb from an ancestral type known as the *pentadactyl* limb (Fig. 116).

The trunk contains a cavity, or *cœlom*, which is occupied by various internal organs, or *viscera*, including the heart, lungs and digestive system. The cœlom contains a watery *cœlomic*, or

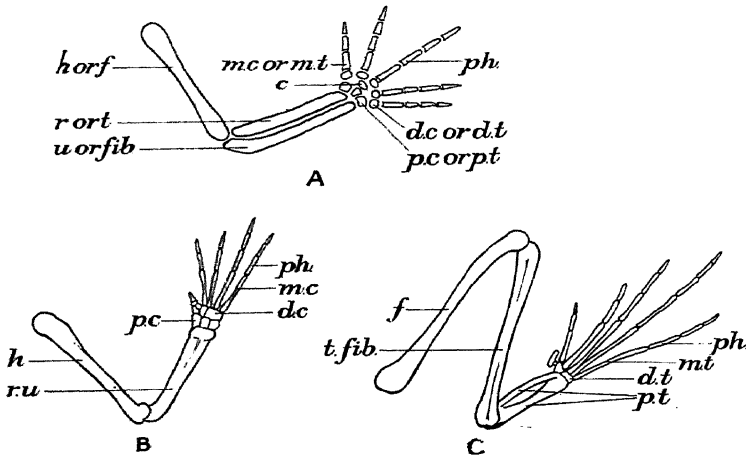


FIG. 116.

A, diagram of the skeleton of a primitive pentadactyl limb; B, skeleton of right fore-limb of the frog; C, skeleton of right hind-limb of the frog.

(c = centrale, f = femur, fib. = fibula, h = humerus, m.c. = metacarpal, m.t. = metatarsal, p.c. = proximal carpal, ph. = phalanges, p.t. = proximal tarsal, r = radius, r.u. = fused radio-ulna, t = tibia, t.fib. = fused tibio-fibula, u = ulna.)

peritoneal fluid, and is lined by a thin membrane, the *peritoneum*, from which folds project into the cavity and support the viscera. The digestive system is supported by the *mesentery*, the reproductive organs of the male frog by the *mesorchium* and those of the female frog by the *mesovarium*.

The Digestive System.

The digestive system, or *alimentary canal*, commences with the mouth and ends at the cloaca. It is essentially a tube through which food passes and into which digestive juices are secreted, and from which digested food is absorbed.

The mouth, bounded by two large jaws which, like those of other vertebrates, open vertically, leads to the *buccal cavity* (Fig. 117). The inner margin of the upper jaws possesses a number of small *maxillary teeth*, which are not used for mastication of food, but merely serve to hold it. On the roof of the buccal cavity are two triangular patches of *vomerine teeth*, in front of which are two small pores, the *internal nares* which communicate with the nostrils of the snout.

Projecting from above into the buccal cavity are two large prominences, marking the positions of the eyeballs, which, unlike those of most vertebrates, are not protected in bony, or cartilaginous, orbits of the skull.

Attached to the front of the lower jaw, and folded backwards along the floor of the cavity, is a forked fleshy tongue. This becomes swollen with fluid and is rapidly projected and retracted during the capture of insects and similar food. Towards the back of the buccal cavity, on each side, is an opening leading to the *Eustachian tube*, which ends below the tympanic membrane, whilst a small slit, the

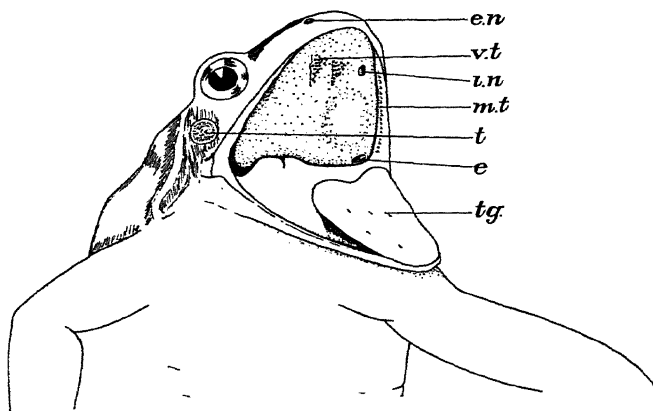


FIG. 117.—Head of Frog showing buccal cavity [$\times 1\frac{1}{2}$].

: opening of Eustachian tube, *e.n.* = external nare, *i.n.* = internal nare, *m.t.* = maxillary teeth, *t* = tympanic membrane, *tg.* = tongue, *v.t.* = vomerine teeth.)

glottis, leads from the floor of the cavity, through a short *larynx*, to the lungs situated in the chest.

The buccal cavity narrows posteriorly to form the throat, or *pharynx*, which continues by a short tube, the *æsofagus*, to the *stomach* lying towards the front of the cœlom.

The stomach, which is slightly swollen, is a receptacle for food in which the first digestive processes are carried out. Its hinder end is constricted by a muscular *pyloric sphincter*, which relaxes periodically to permit food to pass from the stomach to the small intestine. The *small intestine*, continuing directly from the stomach, is some 4 to 5 inches in length. Its first part, the *duodenum*, lies parallel to the stomach, whilst the remainder, or *ileum*, is thrown into several loops, which enables it to be accommodated in the limited space of the cœlom.

The internal surface of the small intestine bears folds, throughout

its length, which serve to increase the area for the final digestion of food, and facilitate the absorption of digested material by the blood.

From the small intestine, the alimentary canal continues as a slightly wider large intestine, or *rectum*, about one inch in length, which passes to the cloaca. The cloaca receives a number of other ducts, including those of the reproductive system and of the bilobed *urinary bladder*, a thin-walled sac situated ventrally at the hinder end of the coelom.

Associated with the alimentary canal are a number of glandular structures concerned in the secretion of digestive fluids into it. These include the *pancreas*, a small cream-coloured body between the stomach and the duodenum, and the *liver*. The liver is a large dark-red organ at the front of the coelom, and is divided into right and left lobes. Between the lobes of the liver is a small green spherical *gall-bladder* which collects and stores *bile*, produced by the liver, and transfers it by a long *bile-duct* to the duodenum. In the frog, the bile-duct passes through the pancreas, and receives from it the *pancreatic juice*, which is delivered, along with the bile, into the duodenum about half-way along its length.

The general processes of digestion¹ taking place in the alimentary canal are as follows. The food captured by the animal receives, in the buccal cavity, a slimy coating of *mucus*, which acts as a lubricant on its passage to the stomach. The stomach-wall secretes *gastric juice* which contains the enzyme pepsin and a small amount of hydrochloric acid. The gastric juice acts as a bactericidal, or sterilising fluid, kills the prey, and, by means of pepsin, digests protein materials to form peptones. During the time that food is in the stomach, the muscular wall contracts and relaxes continuously, causing a thorough mixing of the food with the gastric juice. When the food passes into the small intestine it comes in contact with the *succus entericus*, secreted by the intestinal wall, and the bile and pancreatic juice received from the liver and pancreas respectively. The succus entericus contains several enzymes, including erepsin, which acts on peptones and forms amino-acids, maltase, which acts on maltose to yield glucose, and invertase which acts on sucrose to yield glucose and fructose. It also contains enterokinase, which activates the substance trypsinogen of the pancreatic juice. The pancreatic juice contains amylase, which breaks down starch and glycogen to maltose, lipase which splits fat into glycerol and fatty acids, and trypsinogen. On the entry of trypsinogen into the intestine, it is activated by enterokinase and trypsin is liberated. Trypsin acts on proteins which may have escaped the action of

¹ The digestion of foods and the properties of enzymes are dealt with in Chapter IX.

pepsin, and amino-acids are formed. The bile is a green viscous fluid which aids digestion by assisting in the emulsification of fats, which may then be more readily digested by lipase. The pancreatic juice, in contrast to the gastric juice, is alkaline, and it is only in such a medium that the intestinal enzymes work satisfactorily. The alkalinity of the intestinal contents serves to stop the action of pepsin, which works under acid conditions only.

The digestion of food is completed in the intestine, from which absorption takes place. The intestinal wall is richly supplied with blood-vessels into which most of the soluble food passes. Sugars and amino-acids are carried by the blood to the liver which may transform the sugar to glycogen. Glycerol and fatty acid pass from the intestine into a system of fine lymphatic vessels in which fats are reformed and carried to storage tissues in different parts of the body.

Material which remains undigested, and therefore indiffusible, passes from the small intestine onwards to the rectum, and is periodically evacuated from the cloaca as *fæces*.

Lying in the mesentery, near the commencement of the rectum, is a small round red organ, the *spleen*, which appears to be associated with the alimentary canal. Actually the spleen is part of the blood system and acts as a reservoir of red blood cells. In addition, it is concerned with the destruction of worn-out red blood cells, with the removal of foreign matter from the blood, and in the formation of certain types of white blood cell.

The Circulatory System (Fig. 118).

The conveyance of food material from the alimentary canal to the tissues of the body is carried out by the blood, which is also the means by which soluble waste material is collected up, and by which the gases of respiration are carried.

The blood is circulated in a closed system of blood-vessels, which are connected to a pumping mechanism, the *heart*, which, throughout life, is continuously contracting and relaxing.

The heart (Fig. 119) is situated ventrally at the anterior end of the coelom but is enclosed in a thin membrane, the *pericardium*, which forms a small *pericardial cavity* around it. It consists of a series of chambers which contain blood, a lower *ventricle*, having a thick muscular wall, above which are the thinner-walled *right* and *left auricles*. The auricles are separated from one another by a thin septum, but both communicate with the ventricle through openings provided with *valves*. The blood-vessels connected to the heart either lead blood to it or convey blood from it, and on this feature are described as *veins* and *arteries* respectively.

Passing from the ventricle on the ventral side of the heart is the

truncus arteriosus, which is the main vessel of the arterial system, and on the dorsal side of the heart is a thin-walled triangular compartment, the *sinus venosus*, which receives blood from the body returning to the heart, and passes it into the right auricle. The left auricle receives the union of the two *pulmonary veins* which carry blood from the lungs.

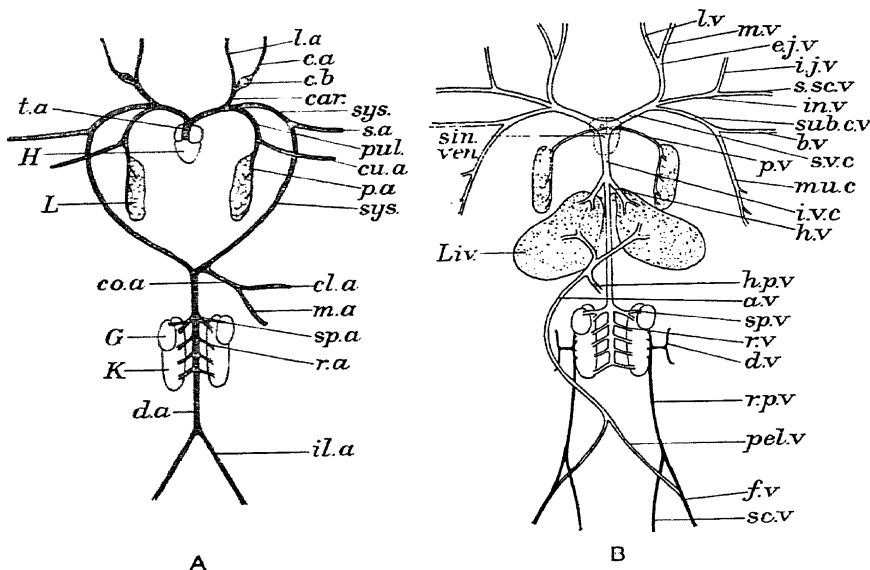


FIG. 118.—Frog. Diagrams of Circulatory System (Ventral Views).
A, Arterial; B, Venous.

(a.v. = anterior abdominal vein, b.v. = brachial vein, c.a. = carotid artery, car. = carotid arch, c.b. = carotid labyrinth, cl.a. = coeliac artery, co.a. = coeliac-mesenteric artery, cu.a. = cutaneous artery, d.a. = dorsal aorta, d.v. = dorso-lumbar vein, ej.v. = external jugular vein, f.v. = femoral vein, G = reproductive organ, H = heart, h.p.v. = hepatic portal vein, h.v. = hepatic vein, il.a. = iliac artery, in.v. = innominate vein, i.v.c. = inferior vena cava, K = kidney, L = lung, l.a. = lingual artery, Liv = liver, l.v. = lingual vein, m.a. = mesenteric artery, m.v. = mandibular vein, mu.c. = musculo-cutaneous vein, p.a. = pulmonary artery, pel.v. = pelvic vein, pul. = pulmo-cutaneous arch, p.v. = pulmonary vein, r.a. = renal artery, r.p.v. = renal portal vein, r.v. = renal vein, s.a. = subclavian artery, s.c.v. = sciatic vein, sin.ven. = sinus venosus, sp.a. = artery to gonad, sp.v. = vein from gonad, s.sc.v. = sub-scapular vein, sub.c.v. = subclavian vein, s.v.c. = superior vena cava, sys. = systemic arch, t.a. = truncus arteriosus.)

Blood consists of a watery fluid, the *plasma*, containing sugars, proteins, and inorganic salts, in which a large number of small cells, the *corpuscles*, occur.

Blood cells (Chap. XX) are of two kinds, viz. red cells, or *erythrocytes*, and white cells, or *leucocytes*. Erythrocytes contain an organic iron compound, hæmoglobin, which is particularly concerned with the carriage of oxygen to the tissues for purposes of respiration.

The white cells vary in form and function, some of them being concerned with the removal of bacteria, and other foreign matter from the body, and are said to be *phagocytic*, whilst others are concerned with the transport of fats. Blood is usually described as *venous* or *arterial*, according to the amount of oxygen carried by its red cells.

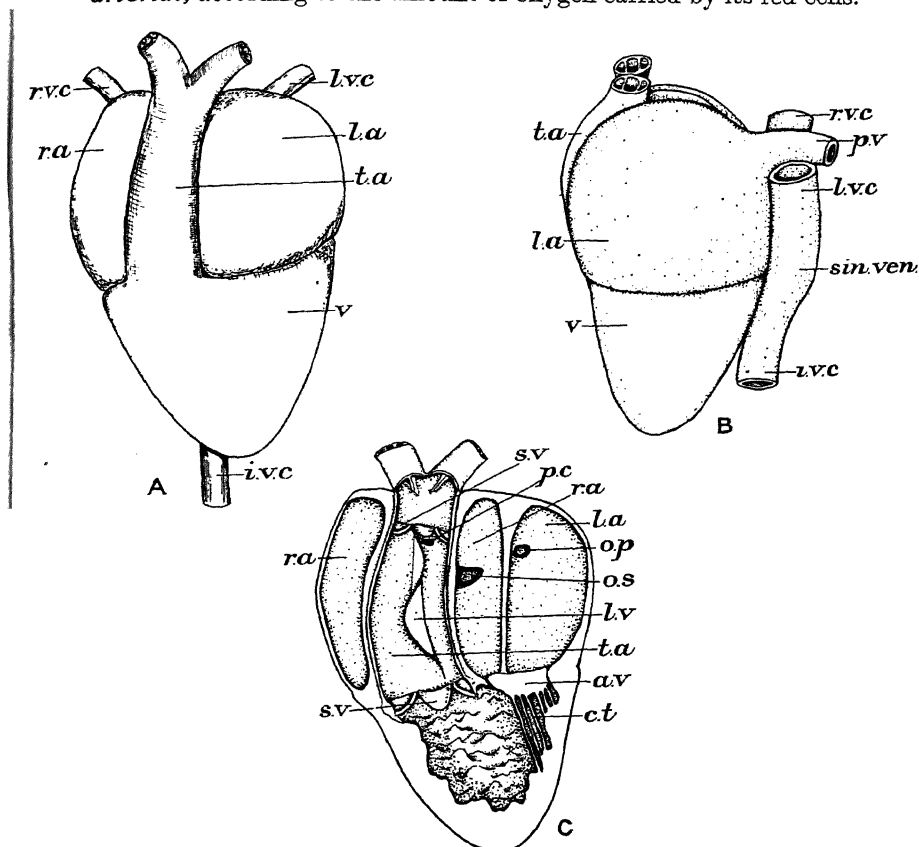


FIG. 119.—The Heart of the Frog [$\times 4$].

A, ventral view ; B, view from left side ; C, section of A, to show internal structure.

(a.v. = auriculo-ventricular valve, c.t. = chorda tendinea, i.v.c. = inferior vena cava, l.a. = left auricle, l.v. = longitudinal (spiral) valve, l.v.c. = left superior vena cava, o.p. = opening of pulmonary veins, o.s. = opening of sinus venosus, p.c. = opening to pulmo-cutaneous arch, p.v. = pulmonary vein, r.a. = right auricle, r.v.c. = right superior vena cava, sin. ven. = sinus venosus, s.v. = semilunar valve, t.a. = truncus arteriosus, v = ventricle.)

Venous blood contains reduced hæmoglobin whereas arterial blood contains fully oxygenated hæmoglobin. In the higher vertebrates, arterial blood is carried in the arteries and venous blood in the veins,

but in the frog this state of affairs is not strictly true. The arterial system commences with the *truncus arteriosus*, which, on passing forward for a short distance, divides into right and left branches. Each branch divides further into three *arterial arches*, the *pulmo-cutaneous arch*, carrying blood to the lungs and skin, the *systemic arch* conveying blood to the main parts of the trunk and limbs, and the *carotid arch* which supplies the head. The systemic artery curves backwards, and, on its way, gives off two branches, the *occipito-vertebral artery* to the skull and spinal column, and the *subclavian artery*, to the fore-limb. The two systemic arteries ultimately unite below the heart, in the middle line, at the back of the coelom, where the united vessel is known as the *dorsal aorta*, but before their union, the left systemic gives off the *cæliaco-mesenteric artery* which supplies blood to the liver, stomach and intestine. The dorsal aorta runs backwards in the trunk, giving off on its way pairs of vessels, the *renal arteries*, to the kidneys, and *genital arteries* to the reproductive organs. It forks at the end of the coelom to form a pair of *iliac arteries* which pass into the hind-limbs.

The carotid arch sends a *lingual artery* to the tongue and throat muscles, and continues forward as the *common carotid artery* which bears a vascular swelling, the *carotid labyrinth*. The common carotid divides to form the *internal carotid artery* supplying the brain, and the *external carotid artery* which supplies blood to the eye region and the mouth.

As the arteries approach the tissues they supply, they divide into smaller branches, or *arterioles*, which, by further division, form minute *capillaries* which are in intimate contact with the tissues. It is from the capillaries that the exchanges between the blood and the tissue cells take place. The capillaries ultimately unite again to form *venules*, which by further unions become the veins leading blood away from the tissues.

The circulatory, or *vascular* system is therefore a closed system, which under ordinary circumstances permits the filtration of fluid to the tissues but prevents the escape of red blood cells.

The venous system, returning blood to the heart consists, of a number of veins which unite to form three large vessels entering the *sinus venosus*.

The blood from the head returns by *right* and *left jugular veins*, and that from the fore-limbs and shoulders by the *subclavian veins*. The jugular and subclavian veins of each side unite to form the *right* and *left superior venæ cavæ*, which pass into the *sinus venosus*. The blood from each hind-limb is returned by two veins, the *sciatic* on the inside, and the *femoral* vein on the outside of the leg. In the trunk the femoral vein divides into a *pelvic vein*

and a *renal portal vein*, the right and left pelvic veins uniting in the middle line on the ventral side of the body and running forward to enter the liver as the *anterior abdominal vein*.

A *portal blood-vessel* is one which does not carry the blood directly back to the heart, but redistributes it in some other organ from which it is ultimately collected for return to the heart. The renal portal vein runs to the outer margin of the kidney of the same side, but before arriving there receives a small *dorso-lumbar vein* from the dorsal body-wall. From each kidney several *renal veins* pass towards the middle and unite between the kidneys to form the *inferior vena cava* which passes forward to enter the sinus venosus. Blood from the stomach, intestine, pancreas and spleen is collected by vessels which form a large *hepatic portal vein* which passes to the liver where the blood is redistributed. From the liver, the blood is passed by a pair of *hepatic veins* which enter the inferior vena cava on its way to the heart.

Venous blood from the muscle-wall of the heart is passed by a small *cardiac vein* into the anterior abdominal vein. The oxygenated blood from the lungs is conveyed by *pulmonary veins* to the left auricle.

The heart is provided with valves, or flaps of tissue, which guard the various openings, and are so arranged that they permit the flow of blood in one direction only. Valves occur between the sinus and the right auricle, between the auricles and the ventricle, and at the exit of the truncus from the ventricle, all arranged to allow blood to flow from the sinus, through the heart and out by way of the truncus.

The truncus arteriosus possesses a specialised structure of importance in the general course of circulation. It is divided longitudinally by a *longitudinal* or *spiral valve* (Fig. 119, c), attached by its length to the dorsal wall, but able to flap freely from left to right ventrally. The upper end of the truncus is guarded by valves, below which is the opening leading to the pulmo-cutaneous arches.

The circulation of the blood is effected by the beating of the heart, which is alternately in a state of contraction, or *systole*, followed by a period of relaxation, or *diastole*.

Venous blood from the body flows into the sinus venosus, which becomes dilated, but then contracts to drive the blood into the right auricle. As the right auricle is filling, the left auricle is also filling with oxygenated blood from the lungs. After dilatation of the auricles, they contract simultaneously, forcing their contained blood into the ventricle, which thus receives both reduced and oxygenated blood. The two types of blood do not, however, mix to any great extent, owing partly to the short time during which they are in con-

tact in the ventricle, and partly to the somewhat spongy wall of the dilated ventricle. The reduced blood lies on the right side of the ventricle, below the exit of the truncus, the oxygenated blood is on the left side, and in the centre is a small quantity of mixed blood.

On the contraction of the ventricle, the reduced blood is the first to enter the truncus, and at this time the longitudinal valve is in the relaxed position on the right side of the truncus. The reduced blood, therefore, passes through the opening of the pulmo-cutaneous arches at the top of the truncus, and is carried to the skin and lungs for oxygenation. As the contraction of the ventricle continues, the remaining blood is forced into the truncus and the longitudinal valve is pushed to the left, so closing the orifice of the pulmocutaneous arches. This results in the blood passing up the truncus to either the systemic or carotid arches. The blood which follows the reduced blood is the partially oxygenated mixed blood, which flows into the systemic arches, as there is less resistance in these than in the carotid arches, which bear the carotid labyrinths. When the ventricle reaches the point of maximal contraction, the force exerted is sufficient to overcome the resistance of the carotid labyrinths, so that the last blood to leave the ventricle, which is the fully oxygenated blood, passes by the carotid arteries to supply the head, and, in particular, the brain.

The mechanism of the frog's heart is simpler than that of such higher vertebrates as the rabbit and man. In these, the reduced and oxygenated blood are separated completely in the heart, and oxygenated blood is distributed equally to the various parts of the body.

The Respiratory System.

Animal respiration is essentially similar to plant respiration, for in both, food materials are broken down with the utilisation of oxygen, to provide energy for growth, movement and other processes.

The normal respiratory process in animals involves the breakdown of glucose, or other simple sugar, and carbon dioxide and water are formed as waste products. Although the process actually occurs in the living cells of the different tissues of the body, the uptake of oxygen and the output of carbon dioxide by the animal are generally the most obvious signs of respiration. For this reason it is usual to consider the gaseous exchanges between the animal and its surroundings as characteristic of the process.

In animals like the frog, the body consists of large numbers of cells compactly arranged into tissues and organs in such a way that direct gaseous exchanges between the cell and the atmosphere are impossible. This necessitates the production of a special system serving to obtain oxygen from the air and to transport it to the

tissues, from which carbon dioxide must be removed and passed out of the body. The blood serves to carry oxygen to the tissues, doing so by virtue of the hæmoglobin of its red cells, which combines readily with oxygen. Carbon dioxide is also removed from the tissues by the blood, being carried mainly by the plasma, which contains salts which combine with the carbonic acid.

The uptake of oxygen by the frog is effected by several organs, a large amount passing into the blood by way of the skin, but some is taken up by special respiratory organs, the *lungs*. The skin is concerned in *cutaneous respiration*, being kept moist by glands to permit the passage of oxygen to the capillaries with which the external skin and the buccal cavity are abundantly supplied. When the frog is under water, and during hibernation, this is the only form of respiration which goes on. *Pulmonary respiration* is carried out by the lungs, which are two thin-walled organs situated at the anterior end of the coelom. Each lung consists of numerous small air-sacs, or *alveoli*, whose walls have a large blood supply. The lungs are connected to the buccal cavity by a short larynx which opens by the glottis.

The *breathing mechanism* of the frog involves the buccal cavity, into which air is first drawn from outside. The mouth is closed, and the floor of the buccal cavity falls, causing air to pass in through the nostrils. The internal nares are then closed, and the floor of the buccal cavity rises to force air through the glottis into the lungs, which become inflated. After a short lapse, the lungs, owing to elastic tissue in their walls, collapse to force the air first into the buccal cavity, from whence it is expelled, through the nostrils, into the atmosphere.

The structure of the lungs is such that they provide an area for gaseous exchange approximately equal to the whole body surface. During its stay in the lungs the inspired air has oxygen removed from it by the blood, which passes out carbon dioxide, to be exhaled with the expired air.

It should be noted that there is no complete removal of oxygen from the inspired air, nor is all the carbon dioxide of the blood passed into the lungs to be expired. The amount of gaseous exchange depends on the activity of the animal, and is sufficient to replenish the blood as it provides oxygen to the tissues, which may require more or less according to conditions.

The Reproductive and Excretory Systems (Figs. 120, 121).

Although the systems concerned with reproduction and the elimination of soluble waste material are quite distinct in function, they are, in common with those of all higher animals, so closely associated as to be considered together as the *urino-genital system*.

The frog is unisexual, so that there are differences in structure between the male and female reproductive systems and their *urinary*, or *excretory system*.

In both male and female, the organs of excretion are the *kidneys*, a pair of red oblong flattened organs situated dorsally outside the coelom, from which they are separated by a thin, transparent membrane. On its ventral surface, each kidney bears an elongated yellow gland, the *adrenal*, or *suprarenal body* which is concerned with the production of a hormone, *adrenaline*, which enters the

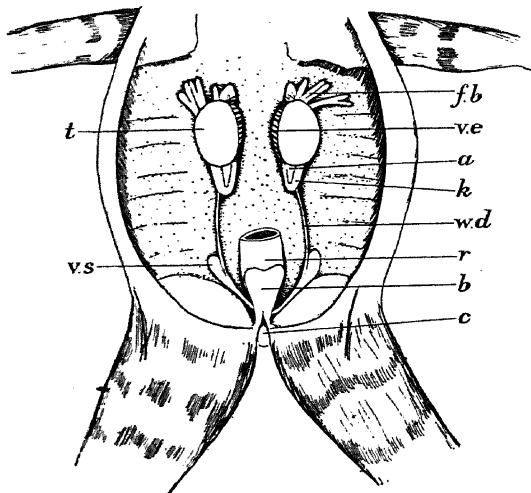


FIG. 120.—Frog. Male Urino-genital System (Ventral View).

t, testis,

blood-stream and causes certain effects in the circulatory system and elsewhere.

The kidney consists of a twisted mass of *uriniferous tubules*, held together by a connective tissue richly supplied with blood-vessels. Each tubule commences blindly as a *Malpighian capsule* (Fig. 122), the side of which is indented and contains a mass of minute blood-vessels, forming the *glomerulus*, which receives blood from the renal artery. The tubules follow a tortuous path through the kidney substance and receive a blood supply from the renal portal vein. The tubules unite to form *collecting-ducts*, which ultimately form the *Wolffian duct*, or *ureter*, which leaves the kidney on its outer margin and runs backwards to the cloaca.

The fluid excreted by the kidney is *urine*, which contains, chiefly

as *urea*, nitrogenous waste matter derived from the amino-acids of the food and the tissues. The urine, after passing down the ureters, is collected by the urinary bladder from which it is periodically voided.

The male organs (Fig. 120) are two *testes* lying close to the kidney, but actually in the coelom, from the dorsal wall of which they are suspended by the thin mesorchium. Associated with each testis is a lobed *fat-body*, which is a reserve of food drawn on by the

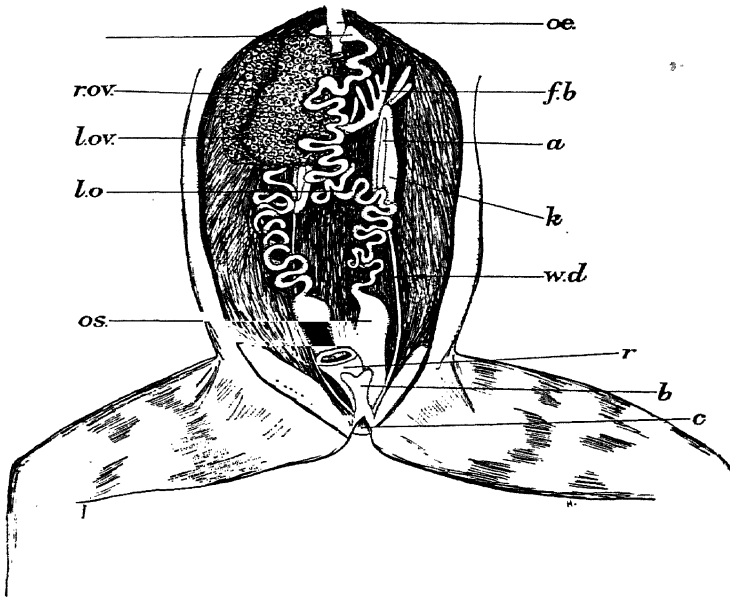


FIG. 121.—Frog. Female Urino-genital System (Ventral View).

(i.o. = internal opening of left oviduct, l.o. = left oviduct, l.ov. = left ovary, displaced to the right side, œ. = œsophagus, o.s. = left ovisac, r.ov. = right ovary; other letters as in Fig. 120.)

animal during hibernation. The testis is composed of a number of *seminiferous tubules* which produce the male reproductive cells, the *spermatozoa*. The spermatozoa pass from the testis in a number of fine ducts, the *vasa efferentia*, to the collecting tubules of the kidney, and therefore pass down the Wolffian duct. Near its lower end the Wolffian duct bears a small swollen *vesicula seminalis*, or sperm-sac, in which the spermatozoa are collected during the breeding season, prior to mating.

In the female frog, the reproductive organs (Fig. 121) are not directly attached to the kidneys. They consist of a pair of *ovaries*

suspended from the back of the coelom by the mesovarium. Each ovary is a mass of dark eggs enclosed in thin connective tissue, and in the breeding season the ovaries are so enlarged as to occupy a large part of the coelom. As in the male, lobed fat-bodies are associated with the reproductive organs.

The eggs are liberated into the coelom, but reach the exterior by way of the *oviducts*, a pair of coiled tubes which commence as small funnel-like openings close to the throat at the front of the coelom, and lead posteriorly to the cloaca. The lower end of the oviduct widens to form an *egg-sac*, in which the eggs remain for a short time before they are laid.

The actual means by which the eggs enter the oviducts is not

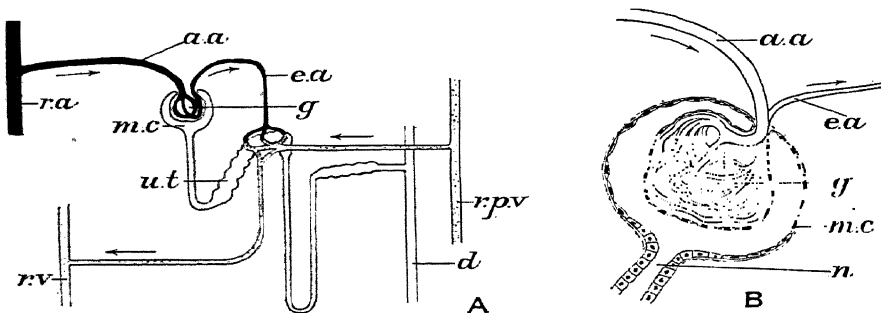


FIG. 122.

A, diagrammatic representation of the blood supply to a uriniferous tubule in the Frog's kidney (arrows denote direction of flow); B, single glomerulus of kidney (enlarged).

(*a.a.* = afferent arteriole of glomerulus, *d* = collecting duct leading to Wolffian duct, *e.a.* = efferent arteriole, *g* = glomerulus, *m.c.* = Malpighian (or Bowman's) capsule, *n* = neck of uriniferous tubule, *r.a.* = renal arteriole, *r.p.v.* = renal portal vein, *r.v.* = renal venule, *u.t.* = uriniferous tubule.)

known, but probably after they are shed into the coelom they are carried by the coelomic fluid, assisted by the ciliated (p. 256) coelomic lining which sets up a forward current. The lining of the oviduct is also ciliated, causing the eggs to move along it, during which they are coated with a slimy material secreted by glands in the wall.

The mating season for frogs in Britain is late March, and in mating the male frog lies on the back of the female, clasping her behind the fore-limbs by means of the swollen pads on his hands.

Spawning takes place in water, and as the eggs pass from the cloaca of the female, spermatozoa are shed over them by the male. A single spermatozoon enters the egg and effects fertilisation, and when the eggs reach the water the slimy coating placed on them in

the oviduct swells to form a clear gelatinous covering which protects the eggs during the time they are hatching.

When the eggs have been in the water for about a fortnight a young tadpole has been formed from each, and this escapes into the water to commence its free existence. The further development of the tadpole occupies about three months, at the end of which it has undergone metamorphosis and become a small frog.

The Nervous System (Fig. 123).

A feature of all animals is the power to respond to environmental stimuli, a general property of protoplasm.

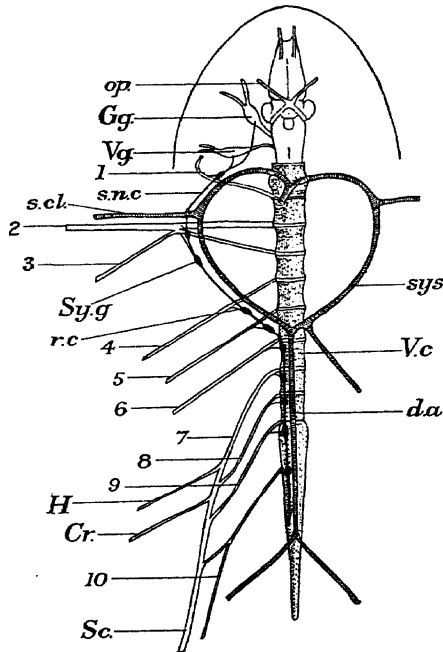


FIG. 123.—Nervous System of the Frog. Diagram to show Spinal Nerves of right side, and their relation to the Sympathetic Nervous System (seen from ventral side).

(Cr. = crural nerve, d.a. = dorsal aorta, G.g. = Gasserian ganglion, H = iliohypoga nerve, op. = optic nerve, r.c. = ramus communicans, Sc. = sciatic nerve, s.cl. = subcl. artery, s.n.c. = sympathetic nerve cord, Sy.g. = sympathetic ganglion, sys. = systemic V.c. = vertebral column, V.g. = vagal ganglion, 1-10 = spinal nerves.)

In the higher animals the perception and transmission of stimuli is confined to the nervous system, which not only acquaints the animal with conditions in its surroundings, but is concerned with the co-ordination of all body movements.

The nervous system of the frog may conveniently be divided into the **central nervous system** and the **sympathetic nervous system**, the former being concerned with special senses and voluntary movements, and the latter with involuntary movements, such as the heart beat and intestinal movement.

The central nervous system consists of the **brain**, occupying the skull, and the **spinal cord**, which is protected by the vertebral column in which it lies.

The brain (Fig. 124) is an elongated hollow organ which consists of fore-, mid- and hind-portions. The **fore-brain** consists of the **cerebral hemispheres** and the **thalamencephalon**, the **mid-**

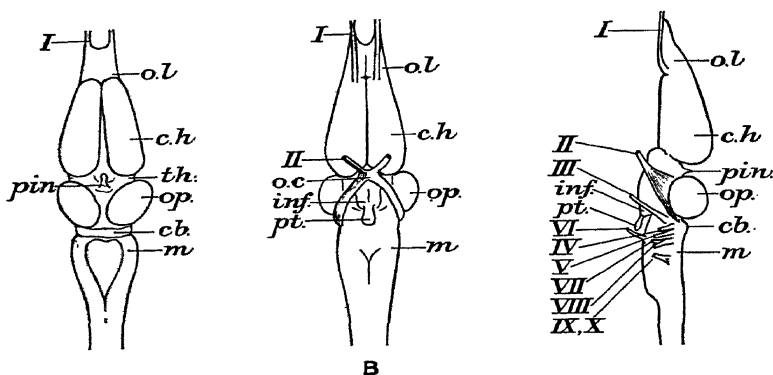


FIG. 124.—Brain of Frog.

A, dorsal view; B, ventral view; C, lateral view.

(*cb.* = cerebellum, *ch.* = cerebral hemisphere, *inf.* = infundibulum, *m* = medulla oblongata, *o.c.* = optic chiasma, *ol.* = olfactory lobe, *op.* = optic lobe, *pin.* = pineal stalk, *pt.* = pituitary body, *th.* = thalamencephalon; I–X, cranial nerves (see text).)

brain of the **optic lobes** and certain associated structures, and the **hind-brain** of the **cerebellum** and **medulla oblongata**.

The cerebral hemispheres are prolonged anteriorly as the **olfactory lobes**, concerned with smell, and overlap the narrow thalamencephalon behind. The thalamencephalon is a small part of the brain, its upper side being covered with a vascular membrane, the **choroid plexus**, through which a small thin **pineal stalk** passes to the inside of the roof of the skull. The sides of the thalamencephalon are thickened to form the **optic thalami**, whilst its floor is drawn out into a hollow **infundibulum** which terminates with the **pituitary body** or **hypophysis**.

The mid-brain bears a pair of prominent optic lobes, and situated on the ventral side between the optic lobes and the cerebral hemi-

spheres is the *optic chiasma* formed by the crossing-over, or *decussation*, of the optic nerves which supply the eyes.

The cerebellum is a small transverse band, immediately behind the optic lobes.

The medulla oblongata is relatively large, being broad in front and narrowing behind to continue as the spinal cord. It is covered dorsally by the posterior choroid plexus.

The brain contains a number of cavities, or *ventricles*, occupied by the *cerebro-spinal fluid*, which is also present in the hollow spinal cord. Each cerebral hemisphere contains an elongated *lateral ventricle* which communicates behind, through a narrow passage, the *foramen of Munro*, with the *third ventricle* situated medially in the thalamencephalon and covered by the anterior choroid plexus. On either side of the third ventricle are the cavities of the optic lobes which open into the *aqueduct of Sylvius*, which leads to the *fourth ventricle* in the medulla. Arising in the brain are several pairs of *cranial nerves*, which pass to the various organs of the head, and, in one case, to other parts of the body. It is difficult to trace the path of these nerves in a dissection of the frog, although their origins, or *roots*, can be located on the brain. The cranial nerves of the frog are as follows:

- I *Olfactory*, supplying the nasal organs in the snout.
- II *Optic*, supplying the retina, or receptive part of the eye.
- III *Oculomotor*, supplying certain eye muscles.
- IV *Pathetic*, supplying an eye muscle.
- V *Trigeminal*, which bears a large *Gasserian ganglion*, and then branches to supply the skin of the front of the head, and the two jaws.
- VI *Abducens*, supplying an eye muscle.
- VII *Facial*, associated with V, and connected to the Gasserian ganglion, and has branches supplying parts of the mouth and throat.
- VIII *Auditory*, supplying the ear.
- IX *Glossopharyngeal*, supplying the pharynx and tongue.
- X *Pneumogastric*, or Vagus, which differs from the other cranial nerves as it takes an extended path to supply various parts of the body remote from the head. The *laryngeal* branch supplies the larynx, the *pulmonary* branch, the lungs, the *cardiac* branch, the heart, and the *gastric* branch, the oesophagus and stomach.

The cranial nerves can be classed on the basis of function into *sensory*, *motor* and *mixed* nerves. Sensory nerves are concerned with the transmission of an impulse initiated in a sense organ, motor nerves transmit impulses from the brain to muscles which respond

and cause movement, and mixed nerves are concerned with both perception and movement. The first, second and eighth nerves are sensory, the third, fourth and sixth are motor, and the remainder are mixed nerves.

The *spinal cord* continues from the medulla, in the backbone, to the extremity of the urostyle, where it ends as an extremely fine *filum terminale*. It is composed of an outer *white matter*, consisting of nerve fibres, and a central *grey matter* consisting of fibres and nerve-cell-bodies (Chap. XX). In transverse section (Fig. 125) the cord is slightly flattened, and is indented above and below by *dorsal* and *ventral fissures*. Arising from the cord is a series of pairs of *spinal nerves*, which emerge between the vertebræ and travel to various parts of the trunk and limbs. Each spinal nerve possesses two roots, the dorsal root bearing a swelling, the *dorsal-*

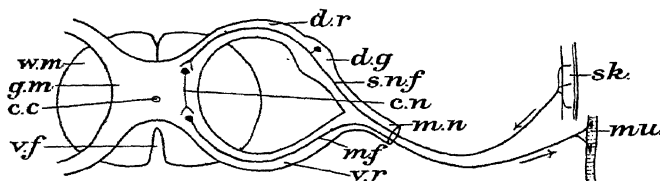


FIG. 125.—Diagram of transverse section through spinal cord of a vertebrate, to show origin of a spinal nerve, and the nerve paths concerned in a simple reflex arc.

(c.c. = central canal, c.n. = connector nerve cell, d.g. = dorsal-root ganglion, d.r. = dorsal (afferent) root, g.m. = grey matter, m.f. = motor nerve fibre, m.n. = mixed nerve, mu. = muscle with endings of motor fibre, sk. = skin with endings of sensory nerve fibre, s.n.f. = sensory nerve fibre, v.f. = ventral fissure of cord, v.r. = ventral (motor) root, w.m. = white matter.)

root ganglion, beyond which the dorsal and ventral roots unite to run from the cord as a mixed nerve.

Nerves are composed of numerous fine nerve fibres, and in the dorsal roots of the spinal nerves, the fibres carry impulses inwards to the cord, whereas the fibres of the ventral root carry impulses from the cord outwards. The dorsal root is, therefore, sensory or *afferent*, and the ventral root motor or *effluent*. If the dorsal root is severed, the animal is deprived of sensation in the parts supplied by the nerve, and if the ventral root is severed, paralysis occurs in the part supplied by the nerve.

There are ten pairs of spinal nerves, the foremost emerging between the first and second vertebræ, and the following eight from between the succeeding vertebræ. The last pair of nerves passes through minute holes in the urostyle. At the points of emergence of the nerves from the spine are white calcareous nodules which may serve for protection. The first spinal nerve is the *hypoglossal*, which runs forward, on the ventral side of the throat, to the tongue. The

second, or *brachial* nerve, passes to the fore-limb, and receives, on its way, a branch from the third nerve, the union forming the *brachial plexus*. The fourth, fifth and sixth nerves are thin, and pass obliquely backwards to various parts of the wall of the trunk. The seventh, eighth and ninth nerves amalgamate in various ways to form a large *sciatic*, or *sacral plexus* which passes towards the hinder end of the coelom. The seventh nerve usually gives off two branches, the *iliohypogastric* and the *crural nerves*, to the hips and ventral body-wall. The main part of the sciatic plexus passes to the hind-limb, as the *sciatic nerve*, receiving on its way the thin tenth nerve, which also sends fine branches to the bladder and cloaca.

The sympathetic nervous system is well defined in the frog, and mainly consists of a pair of grey nerve cords running parallel with the spinal column. These *sympathetic cords* originate, on each side, in the Gasserian ganglion of the fifth cranial nerve, and on emerging from the skull pass backwards along the systemic arches, and the dorsal aorta. They periodically bear small ganglia, at which points they are joined by fine branches, the *rami communicantes*, from the spinal nerves at the same level. From the sympathetic ganglia nerve fibres pass to the viscera, uniting to form various plexuses, including the *solar plexus*, which lies on the dorsal side of the stomach, and sends nerves to the stomach, intestine, liver and other viscera.

The movements produced through the intervention of the nervous system can be classed as either *voluntary*, or *reflex*.

Voluntary actions are those produced at will, and it is usually considered that they are controlled by the cerebral hemispheres.

Reflex actions are not consciously controlled, and are responses to certain stimuli which do not necessarily involve the higher nerve centres in the brain. For example, if the brain of a living frog is destroyed, leaving the spinal cord intact, certain spinal reflexes may be elicited. If a limb is stimulated by acid, or by pinching, it will move in response, and the other limb may attempt to wipe off the acid. For such reflex actions it is necessary to have an *afferent nerve* conveying the impulse from the point of stimulation to the spinal cord, and an *efferent nerve* transmitting an impulse from the cord to the muscles which produce movement, the complete circuit being called a *reflex arc*.

Sense Organs.

Associated with the conscious actions of higher animals are sense organs which contain special types of nerve-endings which respond to one particular stimulus only. In the frog, and similar animals, the senses are connected with sight, smell and hearing.

The **eyes** are the organs of vision, and each consists of a more or less spherical eyeball slightly flattened in front (Fig. 126). The eyeball has an outer coat, the **sense-capsule**, which forms a transparent **cornea** in front, but thickens behind, over the bulk of the eye, as a protective **sclerotic**. The skin in front of the cornea, and closely applied to it, is thin and transparent, being called the **conjunctiva**, which is kept moist by glands. Immediately within the capsule is a darkly pigmented **choroid coat**, which separates from the cornea to form the **iris**, which contains a circular hole, the **pupil**. Behind the pupil is a transparent biconvex **lens**, which serves to focus light on to the sensitive surface at the back of the eye. The space between the cornea and the iris contains a watery **aqueous humour**, whilst behind the lens is a chamber containing a gelatinous **vitreous**

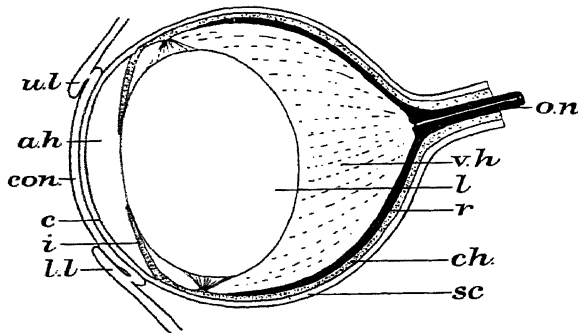


FIG. 126.—Eye of Frog. Diagram of median section.

(a.h. = aqueous humour, c = cornea, ch. = choroid, con. = conjunctiva, i = iris, l = lens, l.l. = lower lid, o.n. = optic nerve, r = retina, sc. = sclerotic, u.l. = upper lid, v.h. = vitreous humour.)

humour. The innermost layer of the posterior chamber is the **retina**, or receptive surface of the eye, which contains nerve-endings upon which the light rays passing through the lens impinge. Nerve fibres run on the outer surface of the retina (i.e. nearest the lens), and collect up as the optic nerve which leaves the eyeball behind, and passes to the brain.

The **ear** of the frog (Fig. 127) possesses no external portion but is completely enclosed in the head. The tympanic membrane is the external boundary of what is known as the **middle ear**, which is limited internally by the **otic**, or **auditory capsule** of the skull. The otic capsule is a cartilaginous compartment containing the **inner ear** which consists of a complicated **membranous labyrinth**. The membranous labyrinth is composed of a sac-like **vestibule**, from the upper part of which arise three curved tubes, the **semicircular**

canals, which are situated in three planes at right angles. The labyrinth is not only concerned with hearing, but also with establishing a sense of balance, this latter function being carried out by the semicircular canals.

The middle ear, or *tympanic cavity*, communicates with the pharynx by the short Eustachian tube. In contact with the tympanic membrane is the free end of a peg-like bony *columella*, the other end of which lies against a thin membrane, the *fenestra ovalis*, covering the outer margin of the otic capsule.

The otic capsule contains a fluid, the *perilymph*, and the labyrinth contains fluid, the *endolymph*. The nerve-endings of the

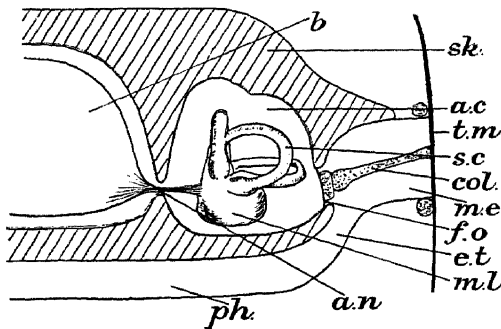


FIG. 127.—Ear of Frog. Diagram of section through the head, to show the right ear from behind.

(a.c. = auditory capsule containing perilymph, a.n. = auditory nerve, b = brain, col. = columella, et. = Eustachian tube, f.o. = fenestra ovalis, m.e. = middle ear, m.l. = part of labyrinth containing endolymph, ph. = pharynx, s.c. = semicircular canal, sk. = skull, t.m. = tympanic membrane.)

auditory nerve are in the vestibule and they receive impulses in the form of vibrations which have been transferred from the tympanic membrane by way of the columella, fenestra ovalis, perilymph and endolymph, and are finally transmitted to the brain as sound.

The *olfactory organs*, or organs of smell, are contained in cartilaginous nasal capsules at the anterior end of the skull. They communicate with the external air and the buccal cavity by the external and internal nares respectively. The capsules are lined with special nerve-endings which are stimulated by particles of matter in the air entering them, and the resultant impulses are conveyed by the olfactory nerves to the cerebral hemispheres.

CHAPTER XX

THE ANIMAL CELL. TISSUES

The animal body is composed of cells essentially like those of the plant, and it is generally believed that the protoplasm of all organisms has the same composition and structure.

The animal cell (Fig. 128, A) is, as a rule, bounded only by the thin plasma-membrane, or *ectoplasm*, within which is a granular cytoplasm containing a nucleus which possesses those features previously described for the plant cell. The cytoplasm contains living and non-living structures, some of which may occur in certain plant cells, but appear to be of general occurrence in animals. Living structures include the *Golgi body*, a tangled mass of fine fibrils, usually close to the nucleus and of a more or less uniform appearance for a particular type of cell, and the *central body*, found immediately outside the nucleus, appearing as a clear space within which lies a minute granule, the *centriole*. The central body plays a part in cell-division, and is absent from cells, such as nerve cells, which do not divide. Non-living inclusions may be food-bodies, such as grains of protein, and droplets of fat and glycogen, and granules of *zymogens*, the precursors of enzymes, and *mucigen*, which gives rise to mucin, the main constituent of mucus.

Cell-division is mainly mitotic (Fig. 128), and though agreeing in its main aspects with that of the plant, differs from it in two respects. The nuclear-spindle arises as an extra-nuclear structure from the centrosome, the centriole of which having divided to initiate the fibres as the two halves separate and pass to the opposite sides of the nucleus. The actual division of the cytoplasm, after the formation of daughter-nuclei by division of the chromosomes, occurs by cleavage, commencing at the periphery and involving the centre of the cell last, in contrast to the cell-plate formation of plants.

Although the typical animal cell has no wall equivalent to the cellulosic membrane of plants, many animal cells do give rise to abundant intercellular substance, in which the original cells become embedded, as in the formation of cartilage and bone. This production of intercellular substance may result in the loss of a cellular

appearance from certain animal tissues, which contrasts strikingly with the obvious cellular structure of plant tissues.

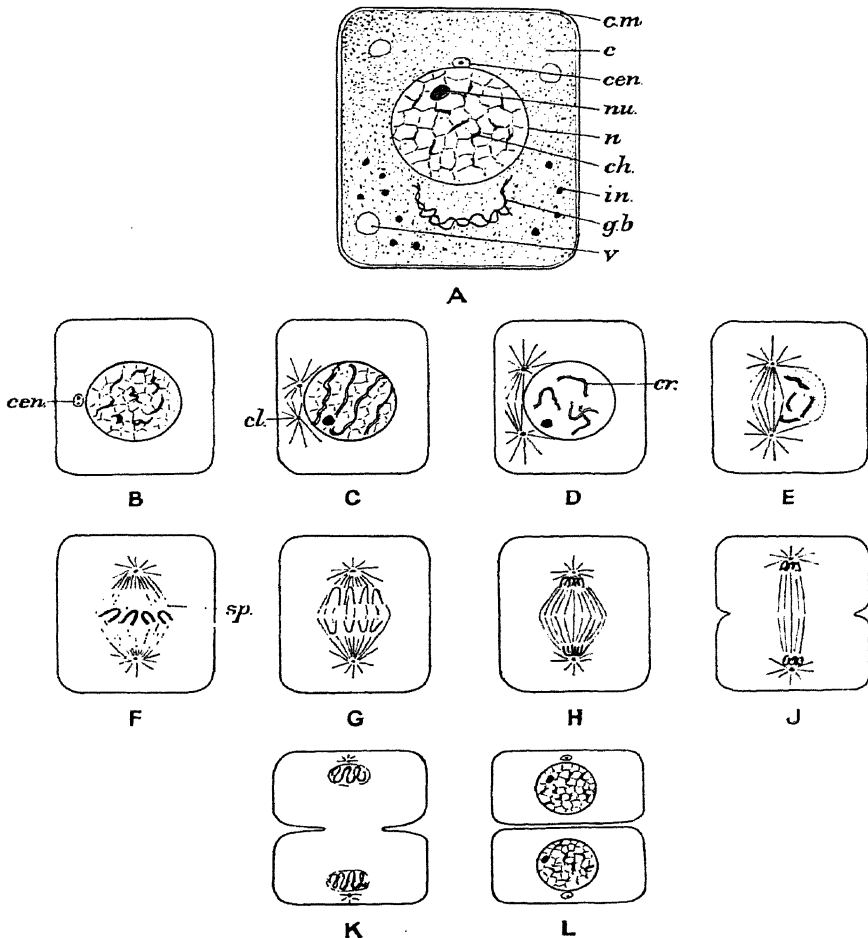


FIG. 128.

A, diagram of an animal cell; B-L, stages in mitosis (diagrammatic).

(*c* = cytoplasm, *cen.* = centrosome, *ch.* = chromatin, *cl.* = centriole, *cm.* = cell-membrane, *cr.* = chromosome, *g.b.* = Golgi body, *in.* = inclusion, *n* = nucleus, *nu.* = nucleolus, *sp.* = nuclear spindle, *v* = vacuole.)

In a multicellular animal, such as the frog or the rabbit, the embryonic animal, developing from the fertilised egg, consists, at an early stage, of meristematic cells of similar appearance. These

dispose themselves to form the three embryonic layers, *ectoderm*, *mesoderm* and *endoderm*, and by their further activities the primary tissues are produced, viz. *Epithelium*, *Connective Tissue*, *Muscle* and *Nervous Tissue*. In the older animal the primary tissues become arranged in various combinations to produce such organs as the skin, lungs, intestines, and so on.

Epithelium consists of cells which retain their cellular appearance, being characterised by the sparsity of intercellular substance, and forms the surface membranes of the body, such as the outer skin, and the linings of the alimentary canal: epithelium may be *simple* or *compound*.

Simple epithelium consists of a single layer of nucleated cells seated on a thin cement-like layer, the *basement membrane*. The cells may be flat, or *squamous*, fitting like tiles to form a thin sheet of tissue, as in the lining of the lung, *cubical* or *columnar* as in the lining of the stomach, or *ciliated*, in which the free surface possesses a fringe of short cytoplasmic fibrils as in the buccal cavity and oviducts of the frog, and the lining of the mammalian trachea. In life, the cilia are in constant motion and produce currents.

Secretory epithelium occurs in many parts of the body, the simplest type being the *goblet-cell* (Fig. 129, Plate V), found amongst the columnar cells of the alimentary canal, producing mucin, which accumulates as a large clear droplet and is finally exuded at the tip of the cell to form mucus. Secretory epithelium may also be arranged in the form of *glands* of various types, such as the peptic gland of the stomach, the cells of which produce both pepsin and hydrochloric acid of the gastric juice.

Compound epithelium may be of two types, viz. *transitional* and *stratified*, and consists of several layers of cells.

Transitional epithelium forms the lining of the bladder and the urinary tract of mammals, and consists of three or more layers of cells which are regenerated from the lowest layer, as the outer cells die and are shed.

Stratified squamous epithelium is the most complex type, and is found as the outer skin, or *epidermis*, of mammals, and forms the lining of the mouth. A section through the epidermis of a mammal (Fig. 130, B) shows the arrangement of the cells into several distinct layers, though these are actually stages passed through as a cell from the lowermost layer, the *stratum germinativum*, gradually passes to the surface and is shed. The stratum germinativum is a meristematic layer, replacing the outer layers by division. Above the stratum germinativum is a layer, the *rete mucosum*, consisting of polygonal nucleated cells with protoplasmic connections; overlying this is the *stratum granulosum*, a



FIG. 129.



FIG. 132.

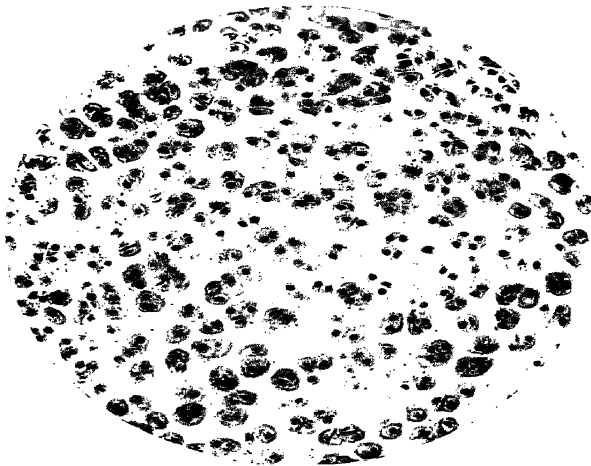


FIG. 134.

FIG. 129.—Photomicrograph of a longitudinal section of small intestine, showing villi with numerous goblet-cells in the columnar epithelial lining.

FIG. 132.—Photomicrograph of a thin film of areolar connective tissue. The broad wavy bands are bundles of white fibres; the thin straighter strands are single elastic fibres.

FIG. 134.—Photomicrograph of a section of hyaline cartilage, showing the cells embedded in the clearer matrix.

few layers of flattened cells containing granules of *eleidin*, then the *stratum lucidum*, a clear structureless layer which is a late stage in the breakdown of the cells as they approach the surface, and finally the *stratum corneum*, a dead layer with a non-cellular laminated structure, consisting of the dead cells or *squames*,

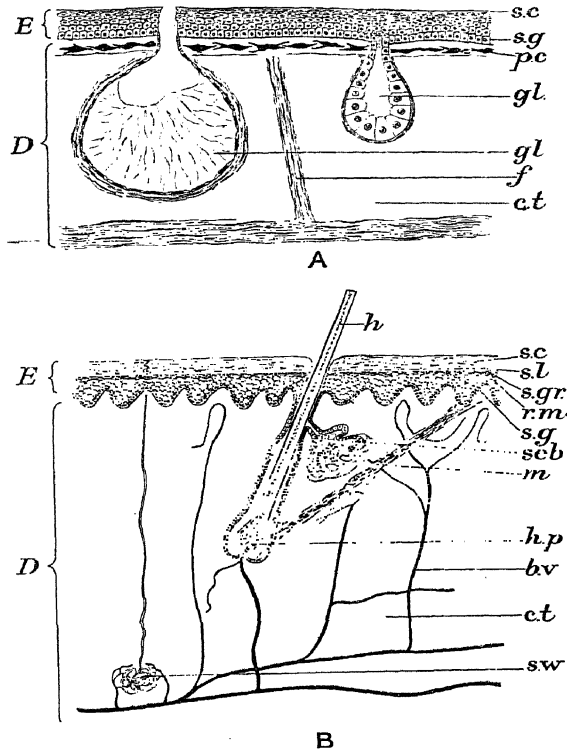


FIG. 130.—Skin (diagrammatic).

A, transverse section of skin of Frog; B, transverse section of skin of Mammal.

(b.v. = blood-vessel, c.t. = connective tissue, D = dermis, E = epidermis, f = fibrous connective tissue, gl. = gland, h = hair, h.p. = hair papilla, m = smooth muscle fibres, p.c. = pigment cells, r.m. = rete mucosum, s.c. = stratum corneum, seb. = sebaceous gland, s.g. = stratum germinativum, s.gr. = stratum granulosum, s.l. = stratum lucidum, sw. = sweat gland.)

which are periodically shed. The stratum corneum forms a suitable protection for animals liable to mechanical and chemical injury.

Connective Tissue also consists of several types which were all originally derived from the primitive connective tissue or *mesenchyme*, a development from the mesoderm of the embryo.

Connective tissue is characterised by the presence of abundant intercellular substance, often greater in amount than the original cells, and may be classified as *Blood and Lymph, Connective tissue proper, Cartilage, Bone*. In the mature animal the interrelations of the various connective tissues are not obvious unless their development in the embryo has been followed, and in the adult the several types cannot be clearly defined. For example, the fibres of loose connective tissue survive in both cartilage and bone and certain chemical substances are common to all three types.

Blood is a fluid tissue, and in Vertebrates consists of a clear, almost colourless fluid, the *plasma*, in which are cells, or *corpuscles* of two main kinds, viz. red cells or *erythrocytes* and colourless (or 'white') cells or *leucocytes* (Fig. 131). The *erythrocyte* of

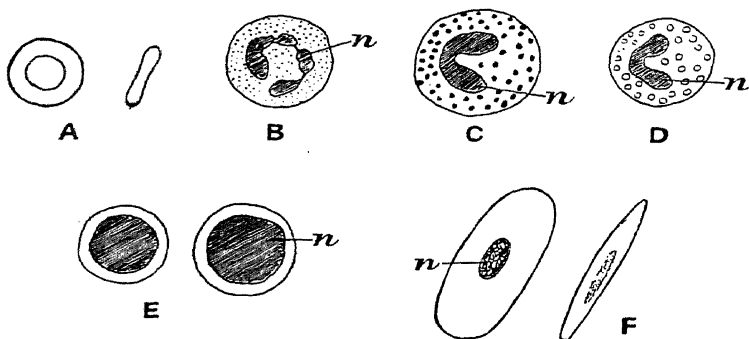


FIG. 131.—Blood Cells (much enlarged).

Human blood : A, red corpuscle, surface and edge views ; B, polymorphonuclear leucocyte ; C, eosinophil leucocyte ; D, basiphil leucocyte ; E, lymphocytes.

Frog Blood : F, red corpuscle, surface and edge views (same scale as A).

(n = nucleus.)

mammals is a circular biconcave cell, (about 0.008 mm. in diameter in man), with a yellowish appearance, devoid of a nucleus, but containing the substance hæmoglobin : in human blood there are some five to five and a half millions per cubic millimetre, and their main importance lies in the carriage of oxygen to the tissues. The *leucocytes* are slightly larger than the red cells, and are not so numerous, man possessing up to eleven thousand per cubic millimetre. There are several distinct types, all nucleated, some being characterised by the presence of stainable granules in the cytoplasm, and most are amœboid, changing their shape from time to time and being capable of migrating from the blood-stream into other tissues. Certain leucocytes are *phagocytic*, ingesting foreign matter, including bacteria, both in the blood-stream, but mainly

in the tissues to which they have passed; other leucocytes, the *lymphocytes*, contain lipases and would appear to be concerned in the fat metabolism of the animal. Besides the two main types of corpuscle, the blood of mammals contains minute colourless nucleated rounded cells, the *platelets*, which are concerned in the phenomenon of clotting, for which reason they are not easily seen outside the blood-vessels unless the blood has been treated to prevent clotting.

The blood of the frog resembles, in all essentials, that of the mammal, save that the erythrocytes are larger, being oval cells up to 0.022 mm. in length, and with obvious nuclei which gives them a biconvex appearance, whilst platelets are replaced by small fusiform (spindle-shaped) cells, the *thrombocytes*.

Lymph is very similar to blood but has no red cells, consisting of a colourless plasma containing leucocytes which are mainly of the lymphocyte type.

Connective tissue proper is characterised by the presence of fibres, amongst which typical cellular elements occur.

Areolar connective tissue (Fig. 132, Plate V) forms the supporting tissue which binds together various structures in the body, such as the thin membrane which attaches the skin of a rabbit loosely to the body-wall. It consists of a more or less amorphous matrix in which is a network of fibres and scattered cells. The fibres consist of single thin *yellow fibres* which branch and anastomose (i.e. join with their neighbours) and broad bands of aggregated *white fibres*. The cells include *fibroblasts*, which lay down *collagen* in their peripheral cytoplasm, and ultimately form new white fibres, *clasmatocytes*, which are irregular nucleated phagocytic cells which ingest foreign particulate matter, *plasma-cells*, with a characteristic granular nucleus, and *leucocytes*, some of which are identical with those of the blood-stream.

Adipose tissue (Fig. 133, A), found, for example, in the subcutaneous tissue of mammals, and the fat-bodies of the frog, is a connective tissue in which the cells store fat. The fat accumulates to form a large vacuole occupying most of the cell, so causing the cytoplasm to appear as a thin ring, thickened only where the flattened nucleus occurs.

White fibrous connective tissue (Fig. 133, B) consists of irregular bundles of white fibres, similar to those of areolar tissue, which are held together by a loose fibrous connective tissue. Such tissue forms the tendons of muscles, and offers resistance to a pulling force, so that when a muscle contracts it exerts its force fully on the bone to which the tendon is attached. As in areolar tissue, the fibres have been formed by previous fibroblasts, which,

as they lay down collagen, become fusiform and lose their cellular appearance, although their presence is indicated by the numerous nuclei seen in the transverse section of a tendon.

Yellow elastic tissue (Fig. 133, c) has the property of yielding readily to a pulling force, but recovers on the release of the tension. It rarely occurs in pure form, but in the ox is found almost pure in

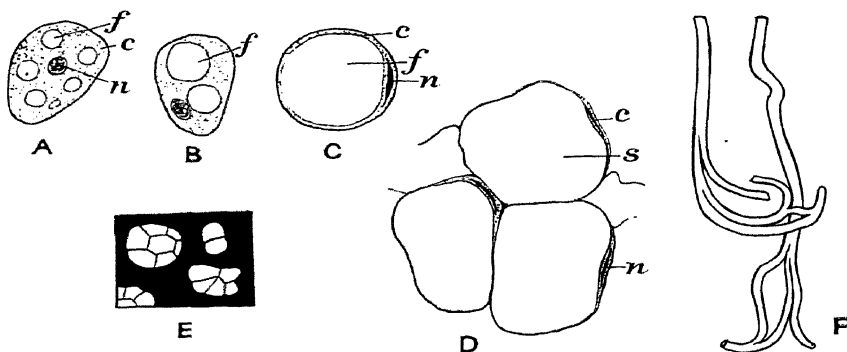


FIG. 133.—Connective Tissue.

A-C, fat-cells, showing stages in the accumulation of fat; D, adipose-tissue, after removal of fat with xylol; E, part of transverse section of Ligamentum nuchæ, showing bundles of elastic fibres; F, elastic fibres from teased Ligamentum nuchæ.

(c = cytoplasm, f = fat-globule, n = nucleus, s = space previously occupied by fat.)

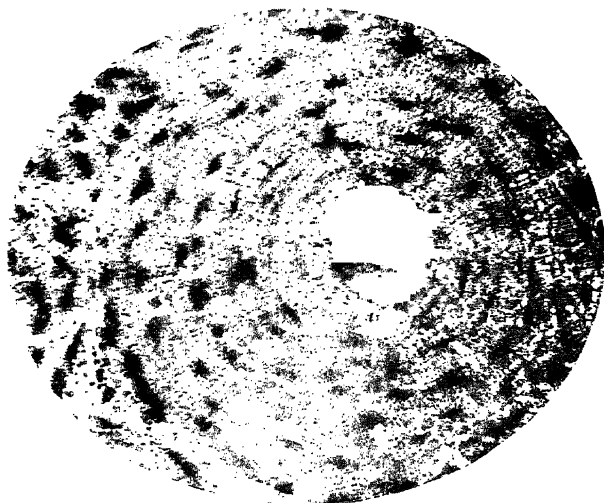
the **ligamentum nuchæ**, a thick ligament in the neck which bears the weight of the head on relaxation of the muscles. Elastic tissue consists of thick yellow anastomosing fibres, which are homogeneous, in contrast to the fibrillar structure of white fibres, and contain **elastin**, which, unlike collagen, is not broken down by acid or alkali.

Cartilage consists mainly of intercellular substance in which are contained the cells which formed it. It forms the skeleton of certain fish, and the skeleton of the tadpole, and most other immature vertebrates which, in the adult stage, have a bony skeleton.

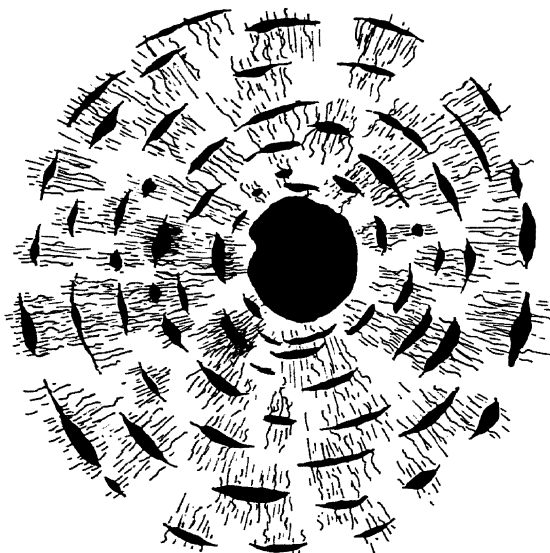
Hyaline cartilage (Fig. 134, Plate V) consists of an opaque greyish matrix (appearing clear in thin sections) scattered through which are the cells containing a nucleus and droplets of glycogen, arranged singly, or in groups resulting from the division of a previous cell. During the transformation of cartilage to bone, calcium salts, especially phosphate, are laid down in the matrix, which becomes granular.

Fibro-cartilage is found in mammals, and consists of cartilage

PLATE VI



A



B

FIG. 135.—Transverse section of one Haversian system in hard bone.
A, photomicrograph; B, diagram of the same, showing the central canal surrounded by the concentric series of lacunæ from which the fine canaliculi pass.

of the hyaline type, of which the matrix has become intermixed with connective tissue fibres.

Elastic fibro-cartilage, found in the external ear, shows the cartilage cells enclosed in capsules in the matrix, which is traversed by yellow fibres ; such cartilage gives greater flexibility to the tissue, for hyaline cartilage alone is of an unyielding nature.

White fibro-cartilage occurs in the intervertebral discs, and consists of bundles of white, collagenous fibres amongst the cells in the matrix ; this tissue is strong but unyielding, and, in the backbone, forms an effective cushion for the absorption of mechanical shocks.

Bone always arises from some other type of connective tissue, and may be either **membrane bone**, or **cartilage bone**, both of which occur in the frog's skull. The former is formed from membranous connective tissue, whilst the latter is a replacement of cartilage. The formation of bone is a complex process, and it must suffice here to mention that bone is laid down by cells, the **osteoblasts**, which are somewhat similar to fibroblasts of areolar tissue. The structure of a typical compact bone may be examined in sections of the limb bones of a mammal, which are examples of cartilage bones. In transverse section (Fig. 135) the bone appears to be composed of a series of circular systems, each consisting of a central canal, surrounded by a number of concentric rings. Each of these systems is a **Haversian system**, the central canal, which carries blood and lymph vessels and nerves, being the **Haversian canal**, and the concentric layers, the **lamellæ**. The lamellæ contain small cavities or **lacunæ**, each of which contains an osteoblast. The osteoblasts possess fine cytoplasmic processes, which run in narrow canals, the **canaliculi**, to the processes of the next osteoblasts, both of the same and of adjacent lamellæ, so forming a continuous network of living substance in the bony matrix. A longitudinal section of the bone differs little from the transverse view, save that the Haversian canals are found to branch and anastomose, forming a nutritional path throughout the bone. The outer surface of the bone is covered by a fibrous tissue, the **periosteum**, which, amongst other things, is concerned with the provision of new osteoblasts.

The limb bone of the frog is somewhat simpler in structure, and though possessing the same essentials is more like a single Haversian system.

Muscular Tissue is specialised for purposes of contraction, for although all living cells exhibit contractility in some degree, those of muscle possess this character in an accentuated form, and are elongated in the direction of the resultant contraction. The types

of muscular tissue are *smooth*, *striated* and *cardiac muscle*, each with their own histological and physiological features.

Smooth muscle, also known as *plain*, *non-striated* and *involuntary muscle*, is concerned with slow rhythmic contractions, and is not usually under direct voluntary control. It occurs in the intestinal walls (where, by its regular contraction and relaxation, it produces the peristaltic movements), in the walls of blood-vessels, and in the skin. The wall of the stomach and intestine of vertebrates possesses two smooth muscle-coats, the inner layer consisting of transversely arranged fibres, the outer layer having the fibres running longitudinally, so that if the transverse section of such an organ (Fig. 136) is examined, the fibres can be seen in both sectional and longitudinal views. The smooth muscle cell is an elongated

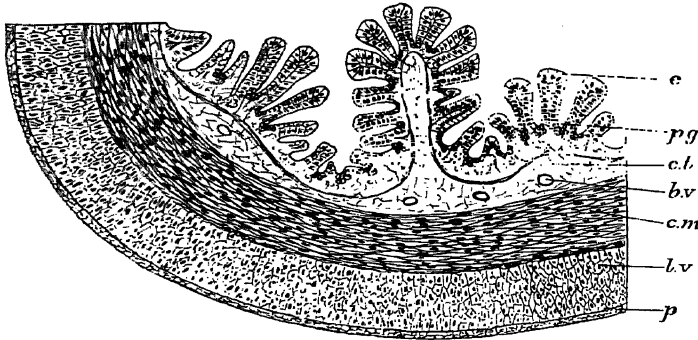


FIG. 136.—Part of a transverse section through Frog's stomach.

(b.v. = blood-vessel, c.m. = circular muscle layer, c.t. = submucous connective tissue, e = columnar epithelium, l.v. = longitudinal muscle layer, p = peritoneum, p.g. = peptic gland.)

spindle-shaped structure with a prominent central nucleus and a longitudinal fibrillar appearance (Fig. 137, D).

Striated or *voluntary muscle* (Fig. 137) forms the bulk of the muscular tissue of vertebrates, and is under voluntary control. Typical voluntary muscle can be seen on skinning the leg of a frog where it consists of spindle-shaped structures with their tapering ends attached by tendons to the bones. Each muscle is surrounded by an elastic connective tissue sheath, the *epimysium* which binds together a number of bundles of fibres, the *fasciculi*, each of which possesses its own sheath or *perimysium*. A fasciculus is a bundle of fibres, between which is a collagenous connective tissue, the *endomysium*. The individual muscle fibre has a longitudinal fibrillar appearance, said to be due to microscopic strands, or *myofibrils*, and is surrounded by a transparent sheath the *sarcolemma*. The most characteristic microscopical appear-

ance of the fibre is, however, the transverse striation, due to alternating light and dark bands, the cause of which has not been satisfactorily explained, though one view is that it is due to short longitudinal units or *sarcomeres*, which are supposed to be the functional elements in contraction. Voluntary muscle effects rapid vigorous movements, in contrast to the leisurely movements of smooth muscle, and it has been calculated that the wing muscles of an insect contract several hundred times a minute during flight. This vigorous contraction involves the expenditure of much energy, and the necessary food is supplied to the muscle by a rich system of capillaries in the sheath between the fibres.

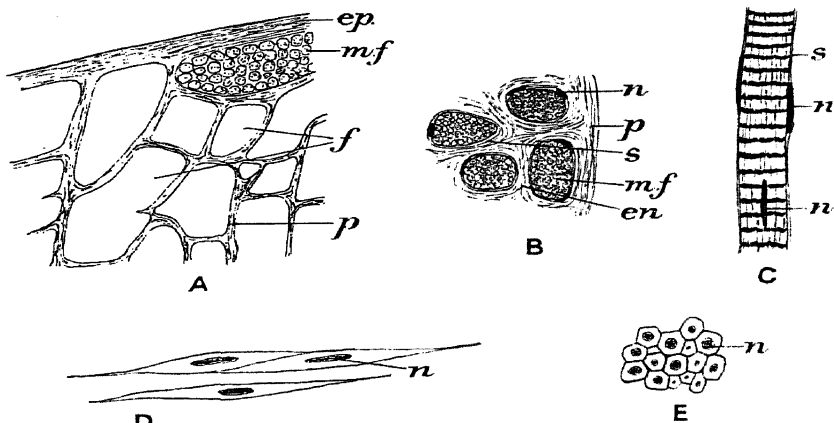


FIG. 137.—Muscular Tissue.

A, part of transverse section of a voluntary muscle (details of one fasciculus shown); B, portion of A, in greater detail; C, single striated muscle fibre; D, smooth muscle fibres; E, smooth muscle fibres in transverse section.

(*e.n.* = endomysium, *ep.* = epimysium, *f.* = fasciculus, *mf.* = muscle-fibre, *n.* = nucleus, *p.* = perimysium, *s.* = sarcolemma.)

In the muscle-fibre substance are numerous nuclei, which are scattered throughout in the frog's muscle, but situated immediately beneath the sarcolemma in that of mammals. As there is no indication of individual cells, the voluntary muscle-fibre is said to form a *syncytium*, or multinucleated cytoplasm which has lost the individuality of the component cells.

Cardiac muscle, such as is found in the walls of the vertebrate heart, has a striated appearance, but is actually involuntary muscle. It consists of short branched cells, with a fibrillar structure and transverse striations, a central nucleus, but no sarcolemma. The fibrils of the branches pass into those of the branches of neighbouring

cells, so producing a tissue which is in some respects a syncytium. Cardiac muscle is the hardest-working tissue of the body as it rests only in the comparatively short period between the heart-beats, which occur continuously throughout life.

Nervous Tissue consists of cells in which the property of conductivity is very pronounced, and which take on the reception of stimuli, transform them into nervous impulses and transmit them to nerve centres. The elements of nervous tissue are the nerve cells, parts of which may be so specialised as to be known as *nerve fibres*.

Nerve cells or *neurons* (Fig. 138) are found in the grey matter of the brain and spinal cord and in certain ganglia. They have a somewhat stellate appearance, possessing a prominent nucleus with a nucleolus, and a number of stainable granules in the cytoplasm, known as *Nissl's granules*, which are probably concerned in the nutrition of the cell, as they may disappear in fatigue and in the degeneration of nerve fibres. The cell possesses cytoplasmic processes which may be short, when they are known as *dendrons*, or elongated, when they are called *axons*, which are actually the main parts of nerve fibres.

Nerve fibres can be classified on the basis of the features of the sheathing membrane. The *medullated* or *myelinated nerve fibre* (Fig. 139) is found in cranial and spinal nerves, and consists of the elongated axon, then known as the *axis cylinder*, surrounded by a thin transparent nucleated sheath, the *neurilemma*. Within the neurilemma is a thick coat of fatty material, the *medullary* or *myelin sheath*, which causes the fibre to have a whitish appearance. The myelin sheath is interrupted at intervals by constrictions, the *nodes of Ranvier*, which occur between the nuclei situated in the *internodes*.

Non-medullated nerve fibres, which are common in the sympathetic nervous system and are seen in certain rami communicantes to which they give a grey colour, are characterised by the absence of a myelin sheath, but possess a nucleated neurilemma.

Nervous transmission is commonly effected by chains of neurons, often with very long axons, which, though not in actual contact, are associated in the spinal cord in a *synaptic junction* formed by short arborisations, the *dendrites*, of one neuron being in close proximity to those of another. The *synapse* transmits stimuli in one direction only, so that in a *simple reflex arc* (Fig. 125), such as is involved in the response of an animal to a pin-prick, a *sensory neuron* receiving an impulse from a sense organ, transmits it, by way of the synapse in the spinal cord, causing a new impulse to pass down a *motor neuron* to the ending in a muscle. Arborisa-

tions may occur between a number of neurons in the cord, so that co-ordinated movements of several organs may result from a particular stimulus.

A *nerve*, or *nerve trunk*, is a collection of nerve fibres outside the central nervous system, arranged into a bundle and bound together by connective tissue. The connective tissue consists of the

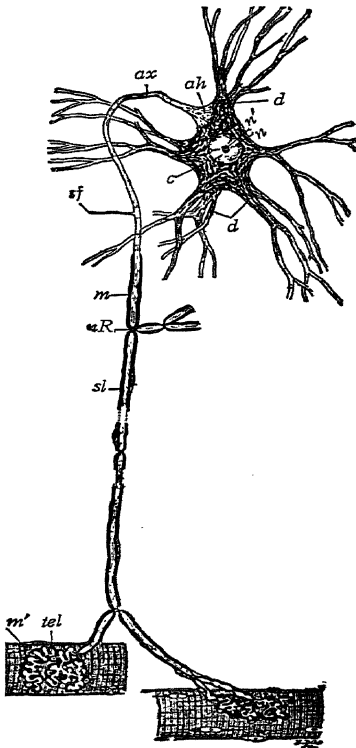


FIG. 138.—Diagram of a Motor Nerve Cell.

(*ax.* = axon, *c* = cytoplasm, *d* = dendrite (short dendron), *m* = myelin sheath, *n* = nucleus, *nR.* = node of Ranvier, *sl.* = neurilemma, *tel.* = ending of axis cylinder in muscle fibre.)

FIG. 139.—Portions of Medullated Nerve Fibres.

(*a* = neurilemma, *c* = nucleus, *R* = node of Ranvier; myelin sheath shown in black.)

endoneurium surrounding the individual fibres, the *perineurium*, which binds together a small bundle of nerve fibres, and the *epineurium*, which contains white fibrous connective tissue and forms the tough outside coat of the nerve.

A ganglion is a collection of nerve cells, usually occurring outside the central nervous system, examples of which were given in the previous chapter.

CHAPTER XXI

PROTOZOA. AMŒBA. PARAMECIUM. COMPARISON OF THE SIMPLE PROTOZOA WITH UNICELLULAR PLANTS

The Protozoa is a phylum consisting of a large number of simple animals, all characterised by a body restricted to a single cell. The group occupies the same position amongst animals as do the unicellular Algæ amongst plants, and it is generally accepted that its members represent the primitive ancestral types from which the higher, more complex animals were evolved.

Amœba (Fig. 140)

Amœba is a simple member of the phylum, belonging to the class Rhizopoda, which is characterised by a special method of movement. It is a microscopic form found in water, and occasionally in the bodies of higher animals.

Amœba proteus is a species occurring in ponds and ditches, either on the muddy bottom or on the surface of water weeds over which it glides by the method of locomotion characteristic of the class to which it belongs.

Microscopically it is seen to be a greyish mass of granular cytoplasm of no fixed shape, but which changes its outline continually during active life. *Amœba* is a single cell, the protoplast consisting of a lighter-coloured cytoplasm and a darker round nucleus. The cytoplasm is differentiated into a thin clear outer layer, the *ectoplasm*, which bounds the more granular inner *endoplasm*. The ectoplasm appears to be delimited on the outside by an extremely delicate membrane, or *pellicle*.

The nucleus displays the usual features, including chromatin and nucleolus.

A number of special structures are present in the endoplasm, one of the most conspicuous being the *contractile vacuole*, a small clear space which disappears at intervals to reappear shortly afterwards in the same position. Small vacuoles containing food particles may also be found in the endoplasm.

Amœba moves from place to place by the formation of finger-like

processes, called *pseudopodia*. Each pseudopodium is initiated at the periphery of the cell, as a small local swelling, which elongates by the extension of the endoplasm into it. The formation of the pseudopodium is complicated, but it involves a protrusion of the pellicle, a liquefying of the endoplasm in order to flow into the protrusion, and a retraction of the cell at a point remote from the new pseudopodium, to supply the material for extension.

The movements of pseudopodia are largely spontaneous, but the

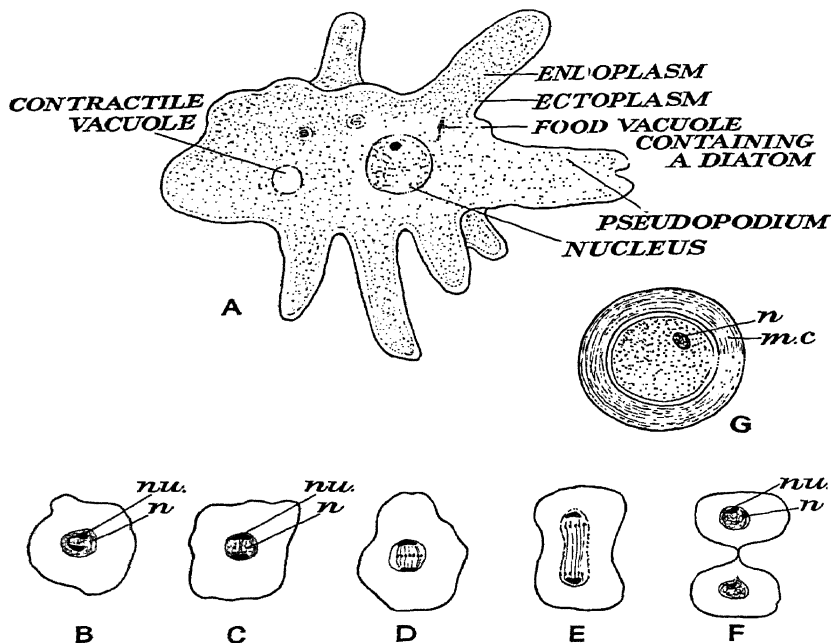


FIG. 140.—*Amoeba*.

A, general features (much enlarged); B–F, reproduction by fission; G, encysted. (*m.c.* = mucous coat, *n* = nucleus, *nu.* = nucleolus.)

organism can react to certain stimuli, and therefore exhibits irritability. When food particles, such as minute Algæ, bacteria, and similar microscopic forms, are in the vicinity, pseudopodia may be formed towards their position.

Food enters the *Amoeba* cell by *ingestion*, one or more pseudopodia flowing round the food particle until it is completely enclosed by the endoplasm (Fig. 141). Once inside the endoplasm, a small vacuole develops round the food, and it seems that digestive fluids are secreted into the vacuole to bring about the simplification of

the contained proteins. The digested material diffuses into the cytoplasm, but any undigestible matter is gradually passed to the surface and egested by a break in the ectoplasm.

Respiration in *Amœba* is simple, and consists of the usual combustion of food in the cell, the necessary oxygen being taken up directly from the water surrounding the animal. The contractile vacuole is an excretory structure, and is probably largely concerned with the elimination of surplus water from the cell. This may be necessary, owing to the sugars, derived from food matter, producing the necessary internal conditions for water to pass into the cell osmotically, through the semipermeable ectoplasm. Other functions suggested include the evacuation of nitrogenous waste matter and carbon dioxide, though the latter, mainly, if not wholly, diffuses from all parts of the cell into the water outside.

The reproduction of *Amœba* is asexual and consists of **binary fission**, in which the parent-cell divides into two (Fig. 140).



FIG. 141.—*Amœba* ingesting food. (Stages in the process are shown from left to right.)

In *Amœba proteus* fission first involves the nucleus, which exhibits a modified form of mitosis, in which the nucleolus divides into two parts which pass to the opposite poles of a simple nuclear spindle. Part of the chromatin then forms a number of small chromosomes which divide, and the halves pass to the opposite poles of the spindle. The nucleus constricts at the equator, and this is followed by a constriction of the cytoplasm to complete the formation of daughter-cells.

When the organism is experiencing conditions unfavourable to active growth, it can enter a resting condition in order to tide over the period. In such cases, the cell becomes more or less spherical and secretes a thick mucous coat, within which are two thinner coats (Fig. 140). The organism is said to be **encysted**, and enters a condition of suspended vitality during which no activities can be observed. The encysted *Amœba* can withstand both freezing and extended drought, and if the pond dries up it is possible for the cyst to be dispersed by the wind and reach more suitable surroundings. On the resumption of favourable conditions, the wall of the cyst bursts open and the organism becomes active again.

Normally, encystment is not a method of multiplication but one of perennation. On some occasions, however, the encysted protoplast divides amitotically to form a number of small uninucleate bodies within the cyst. When the wall of the cyst is ruptured, the small cells, or *spores*, are set free and develop into ordinary *Amœbæ*.

The features of *Amœba* which are representative of the simplest animals may be summarised as follows:

1. It is a unicellular (or non-cellular¹) organism composed of a single protoplast.
2. The organism exhibits no division of labour, for nutritional and reproductive processes are carried out by the same cell.
3. Reproduction is of the simplest kind, viz. direct fission, and the parent protoplasm is shared amongst the offspring, so suggesting the immortality of protoplasm.

Paramecium (Fig. 142)

Paramecium is a member of the class Ciliata, of the phylum Protozoa. It has a more elaborate structure than *Amœba*, from which it also differs in having a body of relatively constant shape.

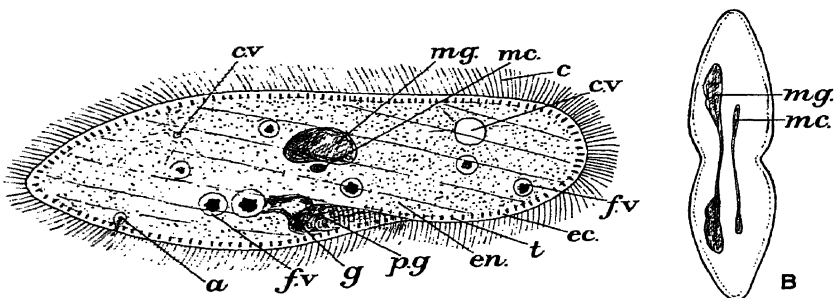


FIG. 142.—*Paramecium*.

A, general features (much enlarged); B, asexual reproduction, commencement of division.

(*a* = temporary anus, *c* = cilium, *c.v.* = contractile vacuole, *ec.* = ectoplasm, *en.* = endoplasm, *f.v.* = food vacuole, *g* = "gullet," *mc.* = micronucleus, *mg.* = meganucleus, *p.g.* = peristomial groove, *t* = trichocyst.)

Paramecium is commonly found in water containing decaying vegetation, and one of the simplest methods of culturing it is to steep some hay in water for about a week, when a copious development of the organisms will have taken place. There are a number

¹ Some zoologists prefer this term, for, as will be seen in considering *Paramecium*, the Protozoa are generally more complicated than *Amœba* and appear to develop specialised organs.

of species of *Paramecium*, but all agree in possessing an elongated oval body, slightly narrower at one end. The organism is somewhat flattened, and has a *peristomial groove* about the middle of one edge, which runs inwards diagonally as the *gullet*. The body is bounded by a thin pellicle, the outer layer of a clear narrow ectoplasm, whilst the endoplasm within has a fluid granular nature.

The surface of the body bears diagonal rows of fine cilia, which are directed towards the more pointed posterior end. By the rapid lashing of the cilia, movement of the organism is brought about, and because of their oblique arrangement the animal moves forward with a spiral movement, revolving about its longitudinal axis.

Two nuclei are situated in the endoplasm, in about the centre of the cell. One nucleus, the *meganucleus*, is large and crescentic, and the other, the *micronucleus*, is commonly situated in the concavity of meganucleus.

Two contractile vacuoles are present, at the anterior and posterior ends of the cell. They are more elaborate than that of *Amœba*, and originate as a stellate group of narrow canals which finally excrete their contents into a central vacuole, which discharges its contents through a break in the surface of the body. The two vacuoles fill and empty rhythmically and, as a rule, alternately.

When attacked, or irritated with such substances as iodine or acetic acid, the cell discharges fine threads over the surface of the body from minute *trichocysts* which lie in the ectoplasm, of which they are a specialised part. The true function of the trichocysts is not known, but, on some occasions, the organism attaches itself, by their means, to more solid structures, and breaks off the threads when it resumes its movement.

Food vacuoles are present in the endoplasm, and originate at the bottom of the gullet. The animal feeds on bacteria and other small particles of organic matter, which are led into the gullet by the current produced by the cilia lining its upper end. On entering the cytoplasm, a small vacuole is formed round the food, and the vacuole is carried through the endoplasm in a path which appears to be constant. During its circulation in the endoplasm, the food is digested, and, as the digested matter is absorbed, the vacuole becomes smaller. Undigestible matter is finally egested from the body through a small break in the ectoplasm, the *temporary anus*. Although little is definitely known about the digestive processes in *Paramecium*, it has been shown, by means of staining the living animal, that the food vacuole is at first acid, but later becomes alkaline. This has led some investigators to believe that there are peptic and tryptic phases in digestion, similar to those in higher animals, which receives some support from the fact that proteins

are readily used up in the cell, whereas higher carbohydrates, such as starch, are not digested, but are egested unchanged, as are fat particles also.

The contractile vacuoles are probably concerned in the excretion of soluble waste material, but also, as in *Amœba*, with the elimination of water. Water enters the endoplasm from the gullet with the food, so that an increase of water occurs in the cell, tending to upset the osmotic equilibrium, which is re-established by excretion.

Respiration is like that of *Amœba*, no special respiratory organs being involved, and the gaseous exchanges taking place directly between the cell and its surrounding water.

Paramecium is dependent on a satisfactory supply of oxygen, and if this is deficient in the water, the organism comes to rest, and its cilia remain inactive until oxygen is again available.

The organism exhibits irritability, being negatively chemotactic to such substances as sodium chloride, moving away from the vicinity of a crystal placed in the water it occupies. It is also *thermotactic*, and varies in its response to heat according to the temperature. It moves away from water at temperatures higher than 30° C., and lower than 20° C., which shows it to prefer an optimum temperature between these limits.

It will be realised from the preceding account, that although *Paramecium* may still be considered to be unicellular, it cannot be considered a simple organism because of the variety of constant structures which it possesses. These structures can hardly be termed organs, although this term is often applied to them, but may be designated *organelles*, or structures of definite function within a cell.

The reproductive processes of *Paramecium* are both asexual and sexual.

Asexual reproduction (Fig. 142) is the usual method of multiplication under conditions favourable for continued growth. It consists of transverse fission, in which the nuclei first divide. The meganucleus becomes elongated and divides amitotically, and, at the same time, the micronucleus divides by mitosis. The cytoplasm constricts below the gullet, and two daughter-cells are formed, each containing two nuclei. Of the two daughter-individuals formed, one possesses the gullet of the parent, whilst the other (posterior) produces a new gullet towards its anterior end.

Because of the behaviour of the two nuclei in asexual reproduction, it is believed that they strictly represent a single nucleus, one part of which (meganucleus) contains vegetative, or somatic material, the other part (micronucleus) containing reproductive material.

PLATE VII

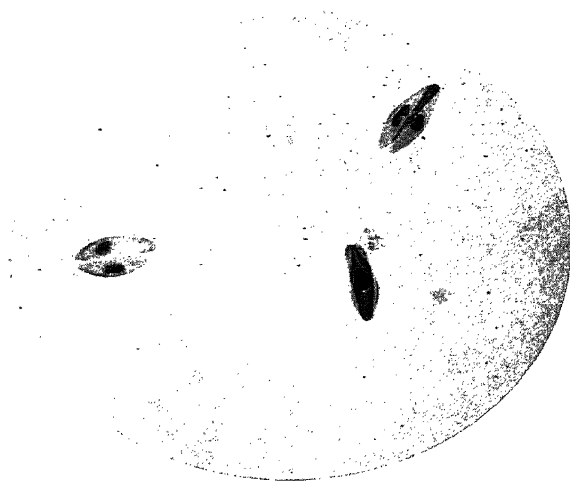


FIG. 143.—Photomicrograph of *Paramecium* in conjugation.

The meganucleus, therefore, controls the general activities of the individual, and the micronucleus, its reproductive processes.

Sexual reproduction (Figs. 143, 144) is called **conjugation** and appears to be essential after a period of continued asexual reproduction, at the end of which the organisms become inactive and are not aroused until conjugation has taken place. During the period of quiescence, individuals become associated in pairs, or **conjugants**, and are united with their peristomial grooves adjacent. The meganuclei gradually disintegrate, and each micronucleus undergoes two divisions to form four. Of the four nuclei in each conjugant, three

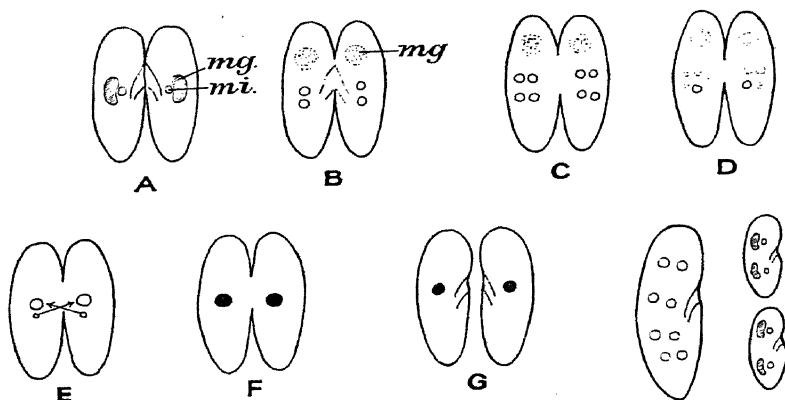


FIG. 144.—Conjugation of *Paramecium* (diagrammatic).

A–F, stages in conjugation (description in text); G, separation of conjugants;

H, diagram illustrating division of an ex-conjugant.

(*mg.* = meganucleus, *mi.* = micronucleus; nuclei which disintegrate are dotted; fusion nucleus, solid; arrows indicate movement of nuclei in fertilisation.)

degenerate and the surviving one divides again to form two nuclei of unequal size.

Fertilisation now occurs by the smaller nucleus of one cell passing to the other cell where it fuses with the larger, passive nucleus.

The fusion-nucleus of each conjugant undergoes three successive divisions to form eight, and the individuals separate, being known, thereafter, as **ex-conjugants**.

Each ex-conjugant divides twice to form four small individuals, each possessing two nuclei. Of the two nuclei contained in each daughter-individual, one becomes the meganucleus and the other the micronucleus, and the organism resumes its active life.

Although *Amœba* and *Paramecium* are animals there is little in their organisation to distinguish them from unicellular plants such

as *Chlamydomonas*. The mode of nutrition of the simple animals and plants is, however, distinctive. Both *Amœba* and *Paramecium* can ingest solid organic matter, which provides their food material, whereas, because of its cellulosic cell-wall, *Chlamydomonas* is unable to do this. On the other hand, because of its chloroplast, *Chlamydomonas* can carry out photosynthesis and build up organic food from simple inorganic material. *Amœba* and *Paramecium* are holozoic, *Chlamydomonas* is holophytic.

It was indicated in an earlier chapter that plants and animals are believed to have had a common origin, and the ancestral form may have combined the characters of the two groups. At the present day there are certain unicellular organisms which exhibit the features of both plants and animals to some extent, and such a form is *Euglena*, common in stagnant water which contains organic matter. *Euglena* is a microscopic organism with an oval body which bears a single cilium, or *flagellum*, at its more rounded, anterior end. The flagellum arises from a small indentation called the gullet. The cytoplasm contains a number of small discoid chloroplasts, and a red eye-spot near the anterior end. When the organism is exposed to light it carries out photosynthesis, but does not form starch from the sugar formed, but small grains of a polysaccharide, *paramylon*. Excretion is effected by a small contractile vacuole which discharges into the gullet.

If *Euglena* occurs in water containing abundant soluble organic matter it absorbs this through the outer pellicle, and may become more or less independent of its chlorophyll.

The so-called gullet of *Euglena* differs from that of *Paramecium* as it is not capable of taking in solid food particles. Whether the gullet was formerly used in feeding is problematic, but if that were the case, the organism would be more animal-like than it now is.

The position of *Euglena*, and similar organisms, in relation to primitive plants and animals, is uncertain. It is sometimes included with the Protozoa, in a class, Flagellata, and with the Algæ in a class Euglenineæ, but it is more satisfactorily considered as a member of a distinct kingdom, the Protista.

CHAPTER XXII

CØELENTERATA. HYDRA

The majority of animals possess bodies composed of cells arranged into definite tissues, and are included in the large division, Metazoa, which contrasts with the non-cellular Protozoa, which do not possess differentiated bodies.

The degree of complexity of the Metazoan body varies considerably, and the group consists of both Invertebrate and Vertebrate types.

One of the simpler Invertebrate phyla is the Cøelenterata, which includes a number of animals not showing much advance on the Protozoa. As an example of the Cøelenterata, *Hydra* will be considered.

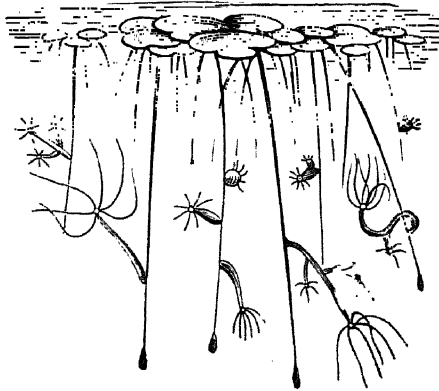


FIG. 145.—*Hydra* attached to a floating aquatic plant (*Lemna*).

Three species of *Hydra* are common in Britain, viz. *Hydra vulgaris*, a colourless, cosmopolitan species, *Hydra fusca*, a brown or reddish species common throughout the Northern Hemisphere, and *Hydra viridis*, a green form with a distribution similar to *H. fusca*.

All are found in fresh water such as ponds, ditches and streams, where they usually live attached to the leaves and stems of water plants (Fig. 145).

Except for their colour, there is little difference between the species, any one of which will serve in illustration of the general characters of the genus.

Examined in water, the animal is seen to possess a thin cylindri-

cal body, about $\frac{1}{4}$ inch in length, the lower end of which is attached to some relatively firm support, whilst the free end bears a fringe of thin outgrowths, the *tentacles*. On closer examination it will

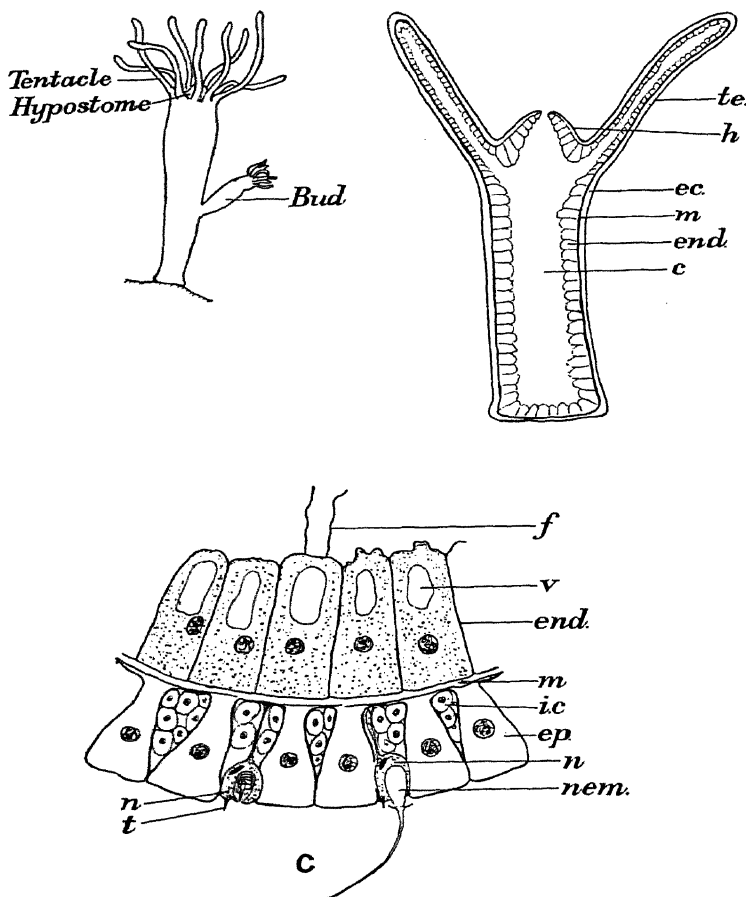


FIG. 146.—*Hydra*.

A, animal, bearing bud (enlarged); B, diagrammatic longitudinal section of body; C, part of transverse section of body-wall (much enlarged).

(*c* = coelenteron, *ec*. = ectoderm, *end*. = endoderm, *ep*. = epithelio-muscular cell of ectoderm, *f* = flagellum, *h* = hypostome, *ic*. = interstitial cell, *m* = mesoglea, *n* = nematoblast, *nem.* = nematocyst, *t* = cnidocil, *te*. = tentacle, *v* = vacuole.)

be found that the tentacles surround a small conical elevation, the *hypostome*, which has, at its centre, a mouth leading to a cavity, the *coelenteron*, in the cylindrical body (Fig. 146).

The lower end of the body is flattened, as the *pedal disc*, the specialised cells of which facilitate the attachment of the organism, without limiting its locomotion.

Hydra responds to stimuli, and is particularly reactive to contact. Under natural conditions the body contracts and elongates, as do the tentacles. If a vessel containing the animal is tapped smartly, the animal retracts its tentacles and contracts its body. The mechanical stimulation of a single tentacle is usually sufficient to elicit a similar response, which indicates that *Hydra* contains some mechanism for the transmission of a stimulus, and the co-ordinated movement in response.

Although commonly found anchored by its pedal disc, *Hydra* is capable of moving from place to place. Its movements, compared with those of *Paramecium*, are leisurely and are more like those of *Amoeba*. It can glide slowly over the surface, to which it is attached, by amoeboid changes in the cells of the pedal disc, but may change its position more quickly either by 'looping,' or 'somersaulting.' When 'looping,' the animal bends its body so that the tentacles form a loose attachment as the pedal disc is loosened and glides to a new point of attachment, closer to the tentacles, after which the process may be repeated.

In 'somersaulting,' the body loops, but the tentacles affix the animal more firmly, whilst the pedal disc is freed, to enable the body to turn over to a point beyond that at which the tentacles are attached, where the disc is re-affixed.

Occasionally *Hydra* may free itself completely from a firm support and float through the water to another region, and it may even suspend itself, tentacles downwards, from the surface film of the water in which it lives.

The tentacles are particularly concerned with obtaining food, such as minute water animals moving in the water around the organism. On such animals brushing against a tentacle, their movements are arrested, and they remain attached to the tentacle, which passes them towards the mouth, often assisted by movements of the other tentacles. The food is passed through the mouth into the coelenteron, or *gastric cavity*, where digestion proceeds.

The cellular structure of *Hydra* is best studied from transverse and longitudinal sections of the body (Fig. 146).

The body and the tentacles are composed of two layers of cells surrounding the central cavity. The outer layer is the *ectoderm* and the inner layer the *endoderm*, the two being separated by a thin layer of intercellular substance, the *mesoglea*, which is of little significance in *Hydra*, but is more abundant in some of the other Coelenterates, such as the jellyfish. The ectoderm is pro-

active, and consists of several distinct types of cell (Fig. 146, c). It is largely composed of columnar *epithelio-muscular cells*, whose inner ends are drawn out as processes, at right angles to the columnar part of the cell, forming a longitudinal reticulation next to the mesoglea. Between the columnar cells are small rounded *interstitial cells* which may replace other cells which have become senile. Some of the interstitial cells become *nematoblasts*, or 'stinging cells,' which are characteristic of the Coelenterates in general. Nematoblasts occur in groups on the tentacles, and also, more dispersed, over the upper part of the body. Each is a cup-like structure, which bears a short process, the *cnidocil*, at its free surface, projecting from the ectoderm. Within the cell is an oval sac, the *nematocyst*, which is a peculiar infolding to form a fine thread, the rest of the sac containing fluid. The cnidocil is sensitive to contact stimuli, and when stimulated, causes the nematocyst to be projected as a fine thread. Several types of nematocyst are found, all being concerned in the capture of prey. One type is barbed, and penetrates the body of the prey, at the same time discharging fluid which renders the prey inactive. Another type has a sticky thread which aids the attachment of prey to the tentacle.

The endoderm consists of columnar cells, somewhat more elongated than those of the ectoderm. Some of the cells are secretory, those in the mouth region secreting mucus, whilst others, more widely dispersed, secrete enzymes into the coelenteron. The majority of the endodermal cells are concerned in nutrition, and have contractile processes at their bases, which run transversely round the body next to the mesoglea. The cytoplasm of these cells is obviously vacuolated, and the free surfaces of the cells bear either flagella or short pseudopodia, the latter being concerned in the ingestion of food particles. It is these cells which give rise to the pigmentation of the coloured species of *Hydra*. In *H. viridis* they are occupied by a unicellular Green Alga, *Zoochlorella*, which is said to live in symbiosis within the animal body. It seems that the algal cells use some of the nitrogenous waste matter, and carbon dioxide of respiration, formed by the animal, which may receive surplus carbohydrate material formed during the photosynthetic process of the Alga. In *H. fusca* the endodermal cells contain small yellowish brown particles of unknown nature.

In addition to the two clearly defined cell layers, certain *nerve-cells* occur next to the mesoglea, below the ectoderm. The nerve-cells have numerous processes, some of which run to the nematoblasts, whilst others are in contact with the processes of the epithelio-muscular cells. This simple nervous network is con-

cerned with the transference of stimuli through the body, with the discharge of nematocysts, and with the movements of the animal.

Body movements are effected by the processes of the main cells of the ectoderm and endoderm, for when the ectodermal processes contract, the body is shortened, but when the endodermal processes contract the body becomes thinner and more elongated.

The digestive system of *Hydra* consists of the coelenteron and some of its lining cells. On the entry of food into the coelenteron, some digestion takes place in the cavity, into which enzymes, secreted by the glandular cells, are passed, and from the cavity soluble material can be absorbed by the lining. As food disintegrates in the coelenteron, small particles may be taken up by the endodermal cells possessing pseudopodia, and digestion then occurs within the cell in a manner not unlike that of the Protozoa.

The transference of food through the body to cells remote from the coelenteron is, presumably, brought about by diffusion through the mesoglea, perhaps assisted by the processes of the ectodermal and endodermal cells.

Undigested waste matter is got rid of through the mouth by contractions of the body-wall.

Respiration is similar to that of the Protozoa, no special system being concerned.

Reproduction in *Hydra* may be asexual or sexual, the asexual method being usual when the animal is living under conditions satisfactory for continued growth.

Asexual reproduction takes place by '*budding*,' in which a new animal arises as a hollow outgrowth from the body of the parent. The bud originates as a slight bulge towards the lower end of the body, and involves both layers of the wall, so that the cavity of the bud is continuous with that of the parent. As the bud enlarges, a ring of short tentacles appears at its free end, followed later by a hypostome bearing the mouth. When ready for shedding, the bud breaks away at the base, the cells of which have closed together to seal the lower end of the coelenteron and form the pedal disc.

Two or more buds may be in process of formation at the same time on one individual and, on rare occasions, the daughter-bud may commence to form a bud before detachment from the parent.¹

Related to asexual reproduction is regeneration, which occurs in many lower Metazoa, and indicates that they are not far removed from the Protozoa. Regeneration consists in the replacement of

¹ In the colonial Coelenterates, such as the marine *Obelia*, the daughter-individuals remain attached to a main stalk, forming a plant-like colony. The buds, in this case, are called *Polyps*, some of which are reproductive, whilst others are nutritional,

a member which may have been detached, or injured. If *Hydra* loses a tentacle, this can be replaced by division of the remaining cells, and if the animal's body is cut transversely into two, each part can grow into a new individual.

Sexual reproduction (Fig. 147) involves the formation of male and female reproductive cells or *gametes*, which are produced by special reproductive organs. *Hydra* is hermaphrodite, one animal forming both male and female organs, although the two types are not usually fertile at the same time, so that cross-fertilisation must take place.

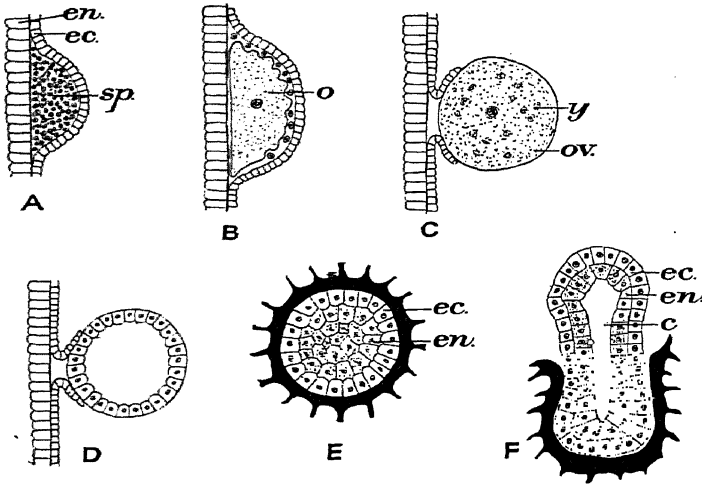


FIG. 147.—Sexual reproduction of *Hydra* (diagrammatic).

A, longitudinal section of testis; B, ditto, of ovary; C, extruded ovum; D, single-layered embryo; E, embryo in spiny shell; F, section of young *Hydra*, on liberation from protective shell.

(c = coelenteron, ec. = ectoderm, en. = endoderm, o = oocyte, ov. = ovum, sp. = spermatozoa, y = yolk granule.)

The male organs, or testes, are produced towards the upper end of the body, arising as small outgrowths mainly by the multiplication of certain interstitial cells. The interstitial cells form a swelling which distends the outer epithelial cells which become the wall of the testis. Each cell within the testis becomes a minute flagellated spermatozoon, which is liberated with its fellows through a small opening at the top of the testis.

The female organs, or ovaries, are usually found near the base of the body. In most cases only a single ovary is formed by one individual, although several testes may arise together. The ovary originates in a similar way to the testis, a group of interstitial

cells being enclosed by the ectodermal wall. In the ovary, however, but one cell (*oocyte*) is fertile, becoming a large ovum, or egg-cell, at the expense of the remaining interstitial cells which it gradually consumes.

The single fertile egg is relatively large, and contains the food material used during the early development of the subsequent embryo. When ripe, the ovary-wall is ruptured and the egg is extruded to the surface, in which position it is fertilised by the entry of a spermatozoon which has swum to the vicinity.

The cell (*zygote*) resulting from fertilisation divides repeatedly to form a spherical group of cells which enclose a central cavity. This is a *blastula*, which, as will be seen later, is a stage in the life-history of all multicellular animals. Some of the cells of the wall of the blastula project into the cavity, and, by further division, fill it completely. The embryo, at this point, consists of an outer layer of cells, representing the ectoderm, and central cells representing the endoderm. A thick warty coat is secreted by the ectoderm, and the protected embryo falls from the parent, and may remain dormant for several weeks or months.

As the sexual process generally occurs towards the end of summer the parent *Hydra* dies shortly after the embryo is freed.

This feature of *Hydra* contrasts with the Protozoa, in which the parent gives rise to offspring which replace it. In *Hydra* it is possible to distinguish *somatic cells*, which are not immortal, but undergo senescence and die, and *germ cells*, which give rise to new individuals and thus perpetuate the species.

After a period of dormancy, the embryo escapes from its protective coat, as an oval body. The cells then differentiate to form the typical body layers, a split arising in the endoderm to produce the coelenteron. Later, the tentacles and mouth are formed and the animal settles down to a normal existence.

The phylum Coelenterata includes the jellyfish, sea anemones and corals. These animals agree with *Hydra* in general structural features, but may differ in shape, size, details of the coelenteron and other features. Some members, including *Obelia*, exhibit an alternation of generations, in which the reproductive organs are formed by a special free-living structure which is distinct from the ordinary somatic phase.

The distinctive feature of the phylum is the body-wall composed of two layers, which forms the wall of a digestive cavity, the coelenteron. Because the bodies of Coelenterates are composed of two layers only, they are said to be *diploblastic* animals, in contrast to the remaining Metazoa which have an additional body layer, the *mesoderm*, and are hence described as *triploblastic*.

CHAPTER XXIII

ANNELIDA. THE EARTHWORM

The Annelida may be taken as a representative triploblastic Invertebrate phylum whose members have a body structure showing an advance on that of the Coelenterates.

It has been seen that the Coelenterate animal is little more than a digestive cavity enclosed by a two-layered wall, the outer layer of which forms the protective skin of the animal.

The triploblastic animals characteristically possess a body-cavity, or coelom, which is not the equivalent of the coelenteron, but is a cavity formed between the outer and inner layers of the body-wall. The coelom is more or less similar in position to the mesoglea of the Coelenterate body, but in the early development of triploblastic animals, cells wander from the two primary layers (ectoderm and endoderm) to form a third layer, the mesoderm. The cells of the mesoderm become modified in many ways, but the total effect is to produce an animal body which possesses a central digestive tract, equivalent to the coelenteron, suspended in the coelom which is bounded, on the outside, by the body-wall.

The Annelida consists, for the most part, of marine worms, but includes the earthworms, which are adapted to a terrestrial existence. The general organisation of the phylum includes the following features :

1. A segmented body, each segment being a *somite*, or *metamere*.
2. An attempt to form a true head at the anterior end of the body, although this is not the case in the earthworms. This feature is called *cephalisation*.
3. The presence of a true coelom in the mesoderm, lined with an endothelium.
4. A central digestive tract, with an anterior mouth and a posterior anus.

In the Annelida, *metamerism*, or body-formation by a series of similar segments, is more pronounced than in any other group. The body is composed of segments which produce an external appearance of annulation, but each segment is separated internally from its neighbours by thin septa, stretching across the coelom

and supporting the alimentary tract. In the more typical members of the phylum, there is a repetition of organs in each segment, but in the earthworm only partial repetition occurs, as the reproductive organs are restricted to certain anterior segments.

The Earthworms belong to an order of the Annelida called the *Oligochæta*, whose members are hermaphrodite animals possessing short bristles or *chætæ*. A common¹ British species is *Lumbricus herculeus*, which is found in pastures, lawns and other places, burrowing in the soil, where it usually remains during the daytime, coming to the surface in the dark or in wet weather. The animal burrows by passing soil through its alimentary canal, ultimately passing it out at the anus in the form of a 'worm cast.' The presence of earthworms in the soil is a benefit to fertility, for not only does the burrowing result in good soil aeration, but during its passage through the body of the animal, the mineral and organic parts of the soil become intimately associated. The animal is sensitive to light, from which it tends to move away, so that it is during darkness that the animal comes to the surface, retreating into the soil if a bright light is directed on to it.

Lumbricus herculeus (Fig. 148) is about 7 inches long, and is composed of some hundred to one hundred and fifty segments. The body is more or less cylindrical, except at the posterior end, where it is flattened dorsiventrally. The upper (dorsal) side of the body is slightly darker than the lower (ventral), and the whole body is protected by a slightly iridescent cuticle. The body can be extended or contracted by means of the muscles of its wall, and by such movements a gliding type of locomotion is effected. In mature worms, a glandular swelling of the body, extending over several segments, is found in the region of segments 31 to 37. This is the *clitellum*, which is concerned in the reproductive process, and, in this worm, takes the form of a saddle-shaped band, not completely encircling the body, but being open on the lower side. Each segment, with the exception of the first and last, bears four pairs of chitinous bristles, the *chætæ*, which are moved by the muscular body-wall. The *chætæ* are directed backwards, as may be ascertained by running the fingers along the body from back to front, and they are concerned with the movements of the worm along the ground, and in its burrow. The surface of the skin of a healthy worm is slimy, owing to a secretion from glandular cells of the epidermis. The slime assists in lubricating the body, but is mainly concerned with keeping the skin moist for respiratory purposes.

¹ Another common earthworm is *Allolobophora terrestris*, distinguished by its prostomium and clitellum, but agreeing in most respects with *Lumbricus*.

THE EARTHWORM

The external features include a number of characteristic apertures and finer pores. A *mouth* is situated in the first segment, being slightly ventral, and having a small projection, the *prostomium*, above it. The prostomium possesses sensory cells which are connected by nerve fibres to the anterior end of the central nervous system. The *anus* is terminal in the last segment, and is the

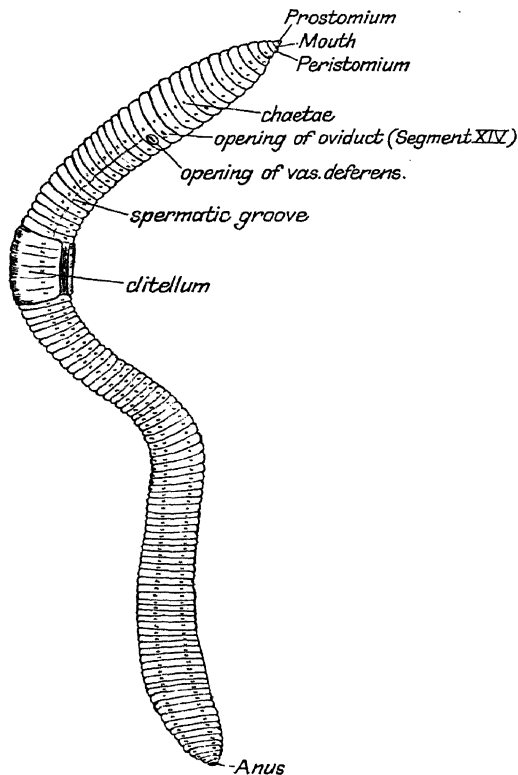


FIG. 148.—The Earthworm (*Lumbricus herculeus*).

External features; anterior part viewed from right side, hinder part viewed ventrally ($\times \frac{1}{2}$).

posterior opening of the alimentary canal, being concerned solely with the evacuation of solid waste matter. In a ventro-lateral position on each segment, excepting the first three and the last, is a pair of excretory pores, or *nephridial apertures*, which are the external openings of special excretory structures occurring in the coelom. Commencing between segments 10 and 11, and con-

tinuing to the posterior end of the body, are small pores, situated singly on the dorsal side in the middle line. These *dorsal pores* communicate with the coelom, and through them the coelomic fluid can escape to the surface of the skin. The external openings concerned with reproduction occur on the ventral side of certain segments. In segment 15, a pair of openings with prominent lips are found; these are the *male apertures*, or openings of the *vasa deferentia*. In segment 14 a pair of small openings indicate the openings of the oviducts of the female reproductive system. Situated between segments 9 and 10, and 10 and 11, are pairs of

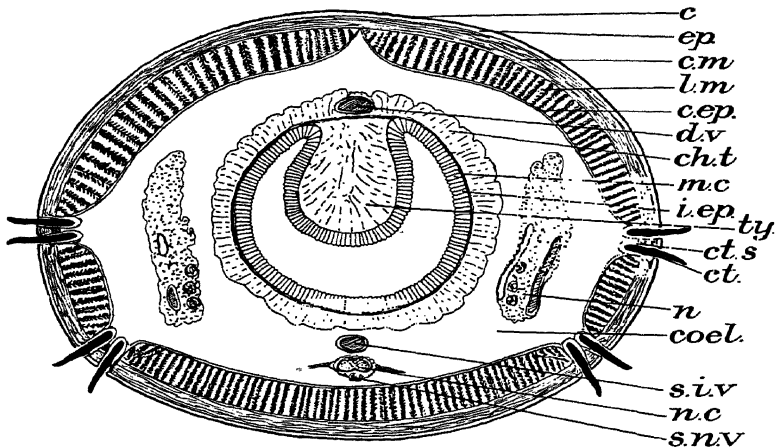


FIG. 149.—Transverse section through the body of the Earthworm, in the intestinal region (semi-diagrammatic).

(c = cuticle, c.ep. = lining of coelom, ch.t. = chloragogenous tissue, c.m. = circular muscle of body-wall, coel. = coelom, ct. = chaeta, ct.s. = chaeta-sac, dv. = dorsal blood-vessel, ep. = epithelial layer of body-wall, i.ep. = epithelial lining of intestine, lm. = longitudinal muscle of body-wall, mc. = muscle layers of intestine, n. = nephridium, and associated tissue, n.c. = nerve cord, s.i.v. = sub-intestinal blood-vessel, s.n.v. = sub-neural blood-vessel, ty = typhlosole.)

small pores which lead to accessory sex organs, the *spermathecae*, which store the spermatozoa from another worm during pairing.

The general organisation of the body may be seen in a transverse section (Fig. 149), which also serves to illustrate the differences between the earthworm, as an Invertebrate coelomate animal, and the frog, as a Vertebrate coelomate animal, and between the earthworm and a Coelenterate animal, such as *Hydra*.

The body-wall is muscular, being bounded on the outside by an epithelial ectoderm which secretes a tough chitinous *cuticle*. Within the ectoderm are two layers of smooth muscle fibres, the outer layer running transversely round the body, and being inter-

rupted by the septa between the segments, the inner layer running longitudinally along the body. On the lateral and ventral surfaces chaetæ may be seen inserted in the muscle layers which serve to move them. The body-wall encloses the coelom, which, in life, contains a clear coelomic fluid containing amoeboid cells. Suspended in the coelom is the alimentary canal, the appearance

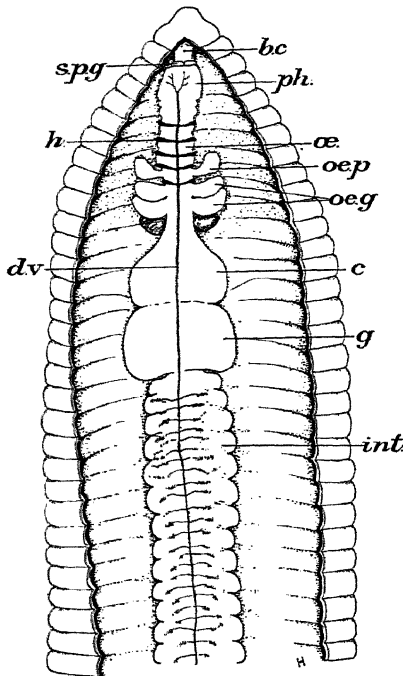


FIG. 150.—The Earthworm. Dissection from dorsal side to show the digestive system (enlarged).

(b.c. = buccal cavity, c = crop, d.v. = dorsal blood-vessel, g = gizzard, h = pseudo-heart, int. = intestine, œ = oesophagus, œ.g. = oesophageal gland, œ.p. = oesophageal pouch, ph. = pharynx, s.p.g. = supra-pharyngeal ganglion.)

extends to segment 6, from whence it continues backwards to segment 15 as a narrow *oesophagus*. Associated with the oesophagus are three pairs of protuberances which contain a white fluid. The first pair, the *oesophageal calciferous pouches*, occur in segment 10, and open into the oesophagus, the remaining two pairs, the *oesophageal calciferous glands*,

of which varies according to the position in which the section has been made. The wall of the alimentary canal consists of an inner epithelial lining, outside which is a layer of smooth muscle running transversely, and a layer of smooth muscle running longitudinally. The organs seen in the coelomic cavity will also depend on the region sectioned, but may include the reproductive organs, and the excretory tubules, or *nephridia*. In any section, the position of the central nerve-cord will be seen, being situated ventrally below the alimentary canal, in contrast to the dorsal position of the central nervous system of the Vertebrate body.

The Digestive System (Fig. 150).

The digestive system is essentially a muscular tube stretching along the whole length of the animal. The anterior mouth opens into a small buccal cavity, the lining of which is thrown into folds. From the buccal cavity the canal continues as a thick-walled muscular *pharynx* which

are situated in segments 11 and 12, or occasionally both in segment 12, and pass their secretion into the calciferous pouches. As these glands contain calcium carbonate, it has been thought that their secretion into the digestive tract is for the purpose of neutralising acid substances in the food passing along the oesophagus. Another view, however, is that the glands remove excess lime from the food, or are concerned with the excretion of carbon dioxide as carbonate. In segment 15, the canal expands to form a muscular *crop*, the walls of which are extensible, so that the organ forms a temporary storage receptacle for food. Behind the crop is another muscular swelling, the *gizzard*, which is lined with a thick secretion, and is concerned with the grinding up of food particles by the coarser mineral particles of the ingested soil. The gizzard occupies segments 17 and 18, and from it, the alimentary canal continues as an annulated *intestine*, which stretches as far as the anus. Projecting into the lumen of the intestine, from the dorsal side, is a longitudinal ridge, the *typhlosole*, which is concerned with increasing the absorptive area of the intestine. The outer layer of the intestinal wall bears a yellowish *chloragogenous tissue*, which is probably concerned with the removal of waste material from the intestine.

The food of the earthworm consists of small particles of vegetable and animal matter in the soil, derived from dead and decaying material. It is sucked into the pharynx, together with other soil particles, and passes along the canal, being moistened by the secretory lining. Temporary storage of the food occurs in the crop, and grinding, which takes the place of mastication, goes on when the food enters the gizzard. The main digestive processes take place in the intestine, from which absorption of digested food by the blood occurs.

Glandular cells occur throughout the length of the alimentary canal, but it seems that the secretion of the intestine alone contains enzymes, the secretion elsewhere consisting of mucus, which acts as a lubricant.

The nature of the intestinal enzymes is not fully elucidated, but there is evidence of trypsin, which may account for the alkaline secretion of the calciferous glands into the oesophagus. From the lumen of the intestine soluble food, resulting from digestion, is absorbed by the epithelial lining, particularly of the typhlosole, which possesses a rich blood supply.

The Circulatory System (Fig. 151).

The earthworm has a closed vascular system of simpler nature than that of the frog. The blood contained in the vessels is bright red, and although it contains various types of leucocytes, has no

red cells. Hæmoglobin, similar to that of the higher animals, is in solution in the plasma.

The blood-vessels cannot be classed as arteries and veins, but the larger ones branch and form a complicated capillary network

A prominent **dorsal blood-vessel** runs along the body above the alimentary canal, and two slightly narrower vessels run along

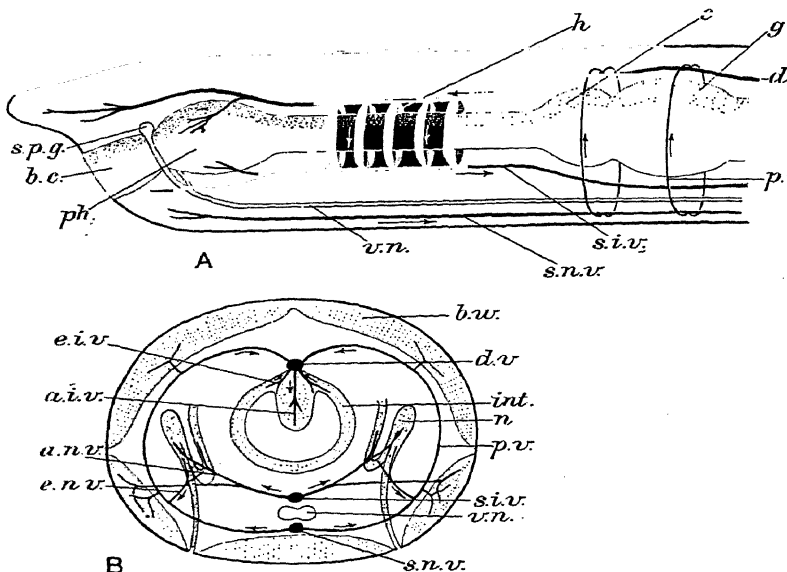


FIG. 151.—The Earthworm. Diagrams of the blood vascular system.

A, longitudinal section of anterior end; B, transverse section in region of intestine. Arrows indicate the direction of flow.

(*a.i.v.* = afferent intestinal vessel, *a.n.v.* = afferent nephridial vessel, *b.c.* = buccal cavity, *b.w.* = body-wall, *c.* = crop, *d.v.* = dorsal vessel, *e.i.v.* = efferent intestinal vessel, *e.n.v.* = efferent nephridial vessel, *g.* = gizzard, *h.* = pseudo-hearts, *int.* = intestine, *n.* = nephridium, *ph.* = pharynx, *p.v.* = parietal vessel, *s.i.v.* = ventral or sub-intestinal vessel, *s.n.v.* = sub-neural vessel, *s.p.g.* = supra-pharyngeal ganglion, *v.n.* = ventral nerve cord.)

the ventral side. The **ventral vessel** is situated between the alimentary canal and the nerve-cord, and the **sub-neural vessel**, as its name implies, lies immediately below the nerve-cord. **Parietal vessels** encircle the segments of the body, connecting the dorsal with the sub-neural vessel, whilst from the ventral vessel, **afferent nephridial vessels** pass to the nephridia, on each side, and, from the nephridia, **efferent nephridial vessels** run to the parietal vessels.

In the region of the oesophagus, there are five pairs of thick-

walled vessels, joining the dorsal to the ventral vessel on each side. The walls of these vessels are contractile and exhibit pulsating movement, and hence the vessels have been called *pseudo-hearts*. The typhlosole is provided with *afferent* and *efferent intestinal blood-vessels*, the former carrying blood from the dorsal vessel and the latter returning blood to it. The outer layers of the body-wall have an abundant capillary supply, for it is by means of the skin that the gaseous exchanges of respiration occur.

The general circulation of blood in the earthworm is simple. Blood flows forward in the dorsal vessel, being permitted to flow in one direction only, because of valves in the vessel. From the dorsal vessel, blood is pumped, by the pseudo-hearts, to the ventral vessel and passes backwards. Some blood passes from the ventral vessel to the nephridia. The blood flow in the sub-neural vessel is also backwardly directed. Blood returns from the sub-neural to the dorsal vessel by way of the parietal vessels, which also send blood to, and receive blood from, the body-wall. Digested food enters the dorsal blood-vessel from the efferent intestinal vessels, whilst some soluble waste material is passed to the nephridia by the afferent nephridial vessels.

The Excretory System.

The excretory system of the earthworm is a comparatively simple system of convoluted tubes, the nephridia, a pair of which occurs in each segment, except the first three and the last. Each nephridium (Fig. 152) is a compactly coiled structure closely attached to the transverse septum, and lying underneath and slightly lateral to the alimentary canal. It commences as a ciliated funnel-like opening, the *nephrostome*, situated in one segment, continuing as a narrow tube, lined with cilia, which passes through the septum into the segment behind, in which the greater part of the organ is found. The coils of the nephridium are embedded in a thin connective tissue abundantly supplied with blood-vessels, and the organ ends with a thick glandular portion and an ejaculatory duct, which passes through the body-wall, to end at the surface as a nephridiopore.

The nephridium is concerned with excretion, probably in two ways. Firstly, by means of its ciliated nephrostome, a current is set up, towards its narrow opening, which serves to pass coelomic fluid into the nephridium, the current being maintained by the ciliated lining of the tube. The coelomic fluid may contain debris from the chloragogenous tissue of the intestine, which may thus be passed from the body. The nephridium is concerned also with the excretion of fluid waste matter, probably as urea, removed from the blood-vessels of the coiled portion of the nephridium.

Respiration.

The earthworm has no specialised respiratory system but depends on direct gaseous exchanges through its moist skin. The vascular system is concerned with the carriage of oxygen to the deeper tissues, and with the removal of carbon dioxide from them. The skin has a rich capillary supply, and the diffusion of gases takes place between the blood and the atmosphere, if the skin is sufficiently

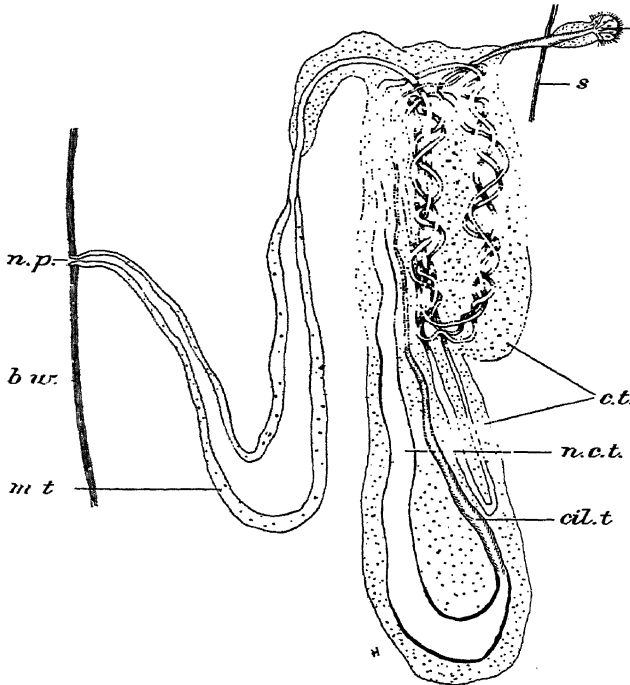


FIG. 152.—A nephridium of the Earthworm.

(*b.w.* = body-wall, *c.t.* = connective tissue carrying blood-vessels, *cilt.* = ciliated portion, *m.t.* = muscular portion, *n.c.t.* = non-ciliated portion, *n.s.* = nephrostome, *n.p.* = nephridiopore, *s* = septum.)

moist to permit the solution of gases. The skin is normally kept moist by mucus from the secretory cells of the epidermis, and by fluid excreted through the dorsal pores. If the body surface is allowed to dry, respiration is prevented, and death soon follows. During extended periods of dry weather, when the soil may be very dry, the worm burrows deeply, and coils itself in a small compartment lined with mucus which serves to keep the worm moist, and to prevent water loss from the soil in that region.

The Nervous System.

The earthworm has a well-defined central nervous system, but simpler than that of the frog, as it consists of a ventrally situated nerve-cord passing longitudinally. The nerve cord actually consists of two closely associated cords below the alimentary canal. The double nature of the cord becomes obvious when the cord is traced forward to the pharynx, where the components separate, and from a collar-like *circum-oesophageal commissure* around the pharynx. The dorsal part of this nerve-collar is formed by two oval swellings, the *cerebral* or *supra-pharyngeal ganglia*, which have been considered to be an attempt to form a simple brain.

From the cerebral ganglia, fine nerves pass forward to the prostomium where they end in tactile sensory cells.

The nerve cord is expanded in the centre of each segment, and from the swelling three pairs of peripheral nerves run out, two pairs entering the body-wall, and the other pair supplying the viscera. Of the two nerves which supply the body-wall on each side, one is sensory, conveying impulses inward from sensory endings in the skin, whilst the other is motor, conveying impulses outwards to the muscles of the body-wall. Therefore, in the earthworm, reflex arcs may be traced. The reflex arc is complete in each segment, but owing to the presence of branched accessory neurons in the cord, the transference of a stimulus between segments is readily accomplished, and can result in a co-ordinated movement of the whole body.

The earthworm has no eyes, ears or olfactory organs, but responds mainly to the stimulus of touch. On the prostomium particularly, but scattered widely over the entire surface of the body, are groups of sensory cells which perceive the stimuli of touch and vibration, to which the animal most readily responds. The animal is sensitive to light, and probably has a sense of smell, but, as yet, the organs concerned are unknown.

The Reproductive System (Fig. 153).

The only method of reproduction carried out by the earthworm is sexual.

The animal shows little power of regeneration, although if the body is severed some distance behind the clitellum, the anterior part can recover and develop as a normal worm, but the hinder portion, although it may show reflex movements for some time, usually dies.

Each earthworm possesses both male and female organs, which can best be seen in an animal with a well-developed clitellum.

The female organs, or ovaries (Fig. 153), are a pair of white

conical bodies suspended from the anterior septum into segment 13. They are ventrally situated, on either side of the middle line, and remain very small until the breeding season. The ovary contains eggs in various stages of development, the ripe eggs being found at the posterior tapering end, from which they are shed into the coelom. From the coelom the eggs are taken into the oviducts and conducted to the exterior of segment 14. The commencement of the oviduct, in the coelom, is a ciliated **oviducal funnel**, immediately behind the ovary. The oviduct may bear a small pouch, the **egg-sac**, in which ripe eggs can be stored for a short time before they are passed to the exterior.

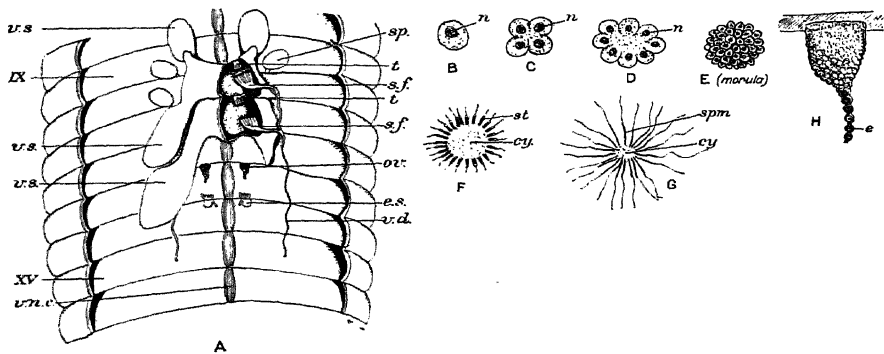


FIG. 153.—The Earthworm.

A, dissection from dorsal surface, to show the reproductive organs: seminal vesicles cut away on the right side to display the testes and sperm funnels; B–G, stages in the development of spermatozoa from a sperm-mother-cell (B), H, ovary, suspended from anterior septum of segment XIII.

(*cy.* = cytophore, or residual cytoplasm, *e* = ovum, *e.s.* = egg-sac, *n* = nucleus, *ov.* = ovary, *s.f.* = sperm-funnel, *sp.* = spermatheca, *spm.* = spermatozoon, *st.* = spermatid, *t* = testis, *v.d.* = vas deferens, *v.n.c.* = ventral nerve cord, *v.s.* = vesicula seminalis; IX, XV = segments.)

The male organs, or testes, are small white bodies, each worm possessing two pairs, a pair in segments 10 and 11, respectively. The testes are attached to the ventral side of the coelom, and from them, sperm-mother-cells are passed into two large lobed sacs, the **seminal vesicles**, overlying, or enclosing the testes. The seminal vesicles are specialised outgrowths of the septa of the segments (10 and 11) in which they occur, but may become greatly enlarged and extend into other segments.

The sperm-mother-cells, or **spermatocytes**, develop in the seminal vesicles. Each first becomes a nodulated multinucleate body, or **morula**, forming uninucleate outgrowths which later become uni-flagellate spermatozoa (Fig. 153, B–G).

In many earthworms, a parasitic Protozoan, *Monocystis*, is found

in the seminal vesicles, developing at the expense of some of the spermatocytes.

In the seminal vesicles are two pairs of *sperm-funnels* with pleated ciliated walls. They are the beginnings of the vasa deferentia, which run backwards, and unite on each side to form a pair of common ducts which open on to the ventral surface of segment 15.

Associated with the true sexual organs are two pairs of spermathecae, developed from the skin between segments 9 and 10. They have no connection with the coelom, but open to the surface of the body by small pores in the grooves between the segments.

Although the earthworm is hermaphrodite, it cannot fertilise itself. Before the eggs can be fertilised, mature worms must become associated in pairs. They pair by partly emerging from their burrows, and lying on the surface of the soil with their anterior ends facing in opposite directions, and their bodies close together, in such a way that segments 9 and 10 of one worm are in close proximity to segment 15 of the other. The worms are held together, for a short time, by a mucous secretion formed by the clitellum of each, and during this time, the spermatozoa are passed from the spermiducal pores of one into the spermathecae of the other.

After pairing, the worms separate, and the act of fertilisation occurs later in each worm. The mucous secretion of the clitellum forms an elastic tube which gradually loosens and slides forward along the body of the worm. As this tube passes over segment 14, eggs are passed into it from the oviducts, and when it arrives at segments 9 and 10, spermatozoa are shed into it from the spermathecae. At this point fertilisation can take place. The mucous tube continues to move forward, carrying its contained eggs, several of which may have been fertilised. In due course the tube passes over the anterior end of the worm, and as it is set free it closes, because of its elastic nature, and is called a *cocoon*. Although the cocoon may contain a number of fertilised eggs, all of which may commence to develop embryos, one worm only continues to develop within the cocoon, from which it later emerges.

CHAPTER XXIV

ARTHROPODA: INSECTA.

THE COCKROACH. THE MOSQUITO

The Insecta is a class of a large phylum, Arthropoda, which also includes the crabs, lobsters and spiders. The Arthropoda is considered to have evolved from an Annelid-like ancestral type, and its members still exhibit some degree of metamerism and possess a double, ventral, ganglionated nerve-cord.

From the point of view of numbers, the Insects constitute the largest class of animals, being specialised for an aerial life, which has involved the development of special respiratory tubules to admit air to the internal tissues.

The majority of insects have the power of flight, a feature of contrast with all other Invertebrates, although some insects, such as the female of certain species of cockroach, do not possess effective wings.

Insects are of great importance both biologically and economically. Reference has already been made to the part they play in the pollination of flowers. Certain insects are the cause of damage to plant crops upon which they feed, locusts doing considerable harm to crops in warmer parts of the world, whilst the larvæ of flies, butterflies, and beetles and adult weevils are the cause of loss of cultivated plants in Britain. Moths, beetles and weevils may be the cause of destruction or deterioration of stored grain and drugs, if precautions are not taken to combat them. The hive bee is of great importance in many parts of the world because of the honey it produces from nectar obtained from various flowers. Drugs derived from the bodies of insects include cochineal, prepared from *Dactylopius coccus*, and cantharidin obtained from a beetle.

A number of insects parasitise the larvæ of other insects, which are ultimately killed. This is of importance when the insect host is a plant pest, such as the larva of the cabbage butterfly, parasitised by an Ichneumon fly, and the white fly, a common pest in green-houses, which may be controlled by a Chalcid parasite, *Encarsia formosa*.

The insect body is typically divided into *head*, *thorax* and *abdomen*, and the thorax bears three pairs of legs, and generally, one or two pairs of wings. The legs are jointed, a characteristic of the phylum Arthropoda.

The life-history of a typical insect involves a *metamorphosis*, which means that the animal changes its form before reaching the adult, or *imago* condition. For example, the cabbage butterfly commences as an egg, which hatches to produce a *caterpillar*, which is the *larval* stage, capable of feeding and movement. On reaching its full size, the caterpillar enters a resting, or *pupal* condition, known as a *chrysalis*, in which the dormant insect is protected by a tough skin. After some time the fully formed butterfly emerges from the chrysalis, leaving the tough skin behind. Flies and beetles have a similar life-history, the larva of the fly being called a *maggot*, and that of the beetle, a *grub*.

The pupal stage of an insect is normally a passive resting condition, but certain insects, including the mosquito and the dragon-fly, have an active pupa, called a *nymph*.

The imago stage of most insects is of short duration, the females laying eggs during this period. The house-fly has a short life-cycle, several generations being produced in one season, but the American locust is said to require seventeen years to become adult.

The Cockroach

The cockroaches belong to an order of Insects called the Orthoptera which differ from the majority of insects as they have an incomplete metamorphosis.

The young insects emerge from the egg-case in a form very similar to the adult, except that they are smaller, and possess no wings. As the insect grows, it periodically sheds its skin, which is an inextensible chitinous investment. The old skin cracks and the insect emerges from it provided with a new skin, which is at first rather soft, but soon hardens. The phenomenon of moulting, common amongst Arthropods, is called *ecdysis*, and in the cockroach there are six or seven moults, carried out over one or two years according to the species. With the final moult the wings appear, in those forms which possess them, the reproductive organs are formed and the insect is a mature adult.

In Britain two species of cockroach are found in houses, often being called 'black beetles,' although not true beetles. They are the common, or Oriental cockroach (*Blatta orientalis*), and the German cockroach (*Blatella germanica*). Other species may be found in warehouses, bakehouses and similar places, and of these, the best known is the American cockroach (*Periplaneta americana*), the largest of the common forms.

None of these insects is a true native of Britain, nor do they live elsewhere than in the vicinity of human habitation. They appear to have been introduced into this country by commerce, being

common pests in ships in which they may have travelled from other parts of the world.

For illustrative purposes the American cockroach will be dealt with, but it should be noted that, in this insect, both sexes are winged, and of the same general appearance, whereas, in the common cockroach, the female has only rudimentary wings, and the abdomen is broader than that of the male.

The American cockroach (Fig. 154) is of a dark brown colour and reaches a length of about $1\frac{1}{2}$ inches. Its body is clearly divided into an oval head, attached by a thin neck to the thorax which continues backwards as the abdomen. The thorax and abdomen

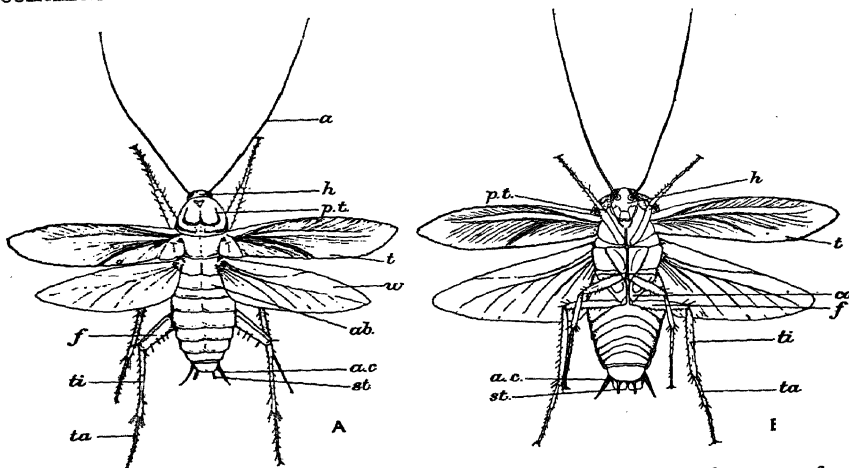


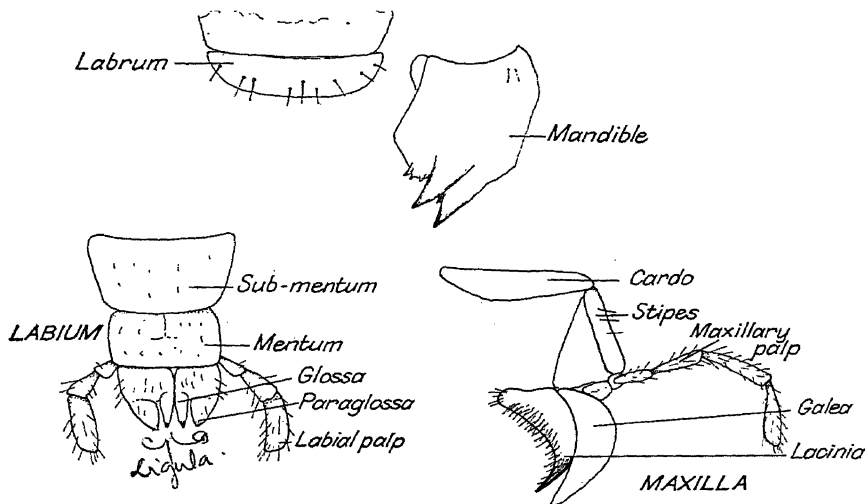
FIG. 154.—The Cockroach (*Periplaneta americana*). External features of male insect [$\times \frac{3}{4}$].

A, dorsal view; B, ventral view.

(a = antenna, ab. = 1st abdominal segment, a.c. = anal cercus, co. = coxa, of 3rd left leg, pt. = prothorax, st. = anal styles, t = tegmen, ta. = tarsus, ti. = tibia, of 3rd left leg, h = head, f = femur, of 3rd left leg, w = flight wing.)

are flattened dorsiventrally, and are protected by a series of plates of chitin which form an external protective *exoskeleton*. The head is flattened from back to front and appears to be at right angles to the rest of the body. The mouth opens below the head and is provided with biting jaws which move sideways. The parts of the mouth (Fig. 155) are somewhat complicated, and consist of a number of articulated chitinous segments. The *labrum*, or upper lip, hangs from the front of the head, and behind it is a pair of serrated jaws, or *mandibles*. Behind each mandible is the *first maxilla*, bearing a jointed appendage, the *maxillary palp*. The lower lip, or *labium*, on the posterior aspect of the mouth, is

formed by the fusion of the *second maxillæ*. It consists of a broad base, the *submentum*, and a smaller, distal *mentum*, to which are attached the jointed *labial palps*, the *glossæ* and the *para-glossæ*, the last two together forming the *ligula*. The head is protected externally by chitinous plates fitting closely together, and consists of segments, as shown in Fig. 156. Two large *compound eyes* are situated laterally near the upper side of the head, and on the front of the head are two whitish spots, the *fenestræ*, which, in some species, are replaced by simple eyes, or ocelli. Close to each fenestra, is a long jointed *antenna*, a tactile and olfactory sense organ which the animal waves about during active life.



. 155.—The appendages of the mouth of the Cockroach (dissected and enlarged).

The thorax is composed of three segments, protected by thick rings of chitin. The dorsal part of each ring is the *notum* or *tergum*, and the ventral part, the *sternum*. Between the rings of chitin are thin bands of cuticle which permit body movement. The foremost segment of the thorax is the *prothorax*, the pronotum of which is large and projects anteriorly to conceal and protect the thin neck. On occasions, the head may be retracted beneath the pronotum. The second thoracic segment, the *mesothorax*, bears the wings, of which there are two pairs, the fore-wings, or *tegmina*, being dark-coloured, and forming a protection for the thin, transparent flight wings behind, which are folded along the back of the insect when it is at rest. Although provided with wings, the cockroach rarely resorts to flight but depends on its running powers for

moving quickly. The hindermost thoracic segment, the *meta-thorax*, is smaller and less specialised than the other two.

Attached to the ventral side of each thoracic segment is a pair of walking-legs. The leg is composed of several joints, and terminates distally in a pair of hooked claws, which enable the insect to climb, and a suctional pad which prevents slipping.

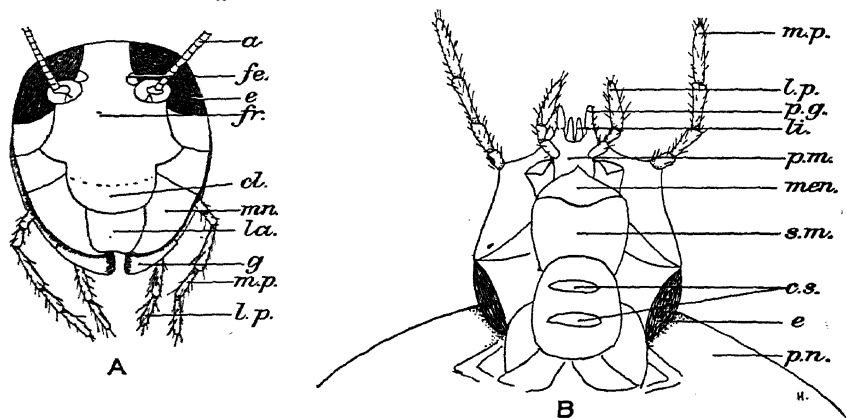


FIG. 156.—The head of the Cockroach (*Periplaneta*) (enlarged).

A, anterior view; B, view of under side.

(a = antenna, cl. = clypeus, c.s. = cervical sclerites, e = compound eye, fe. = fenestra, fr. = frons, g. = galea of maxilla, la. = labrum, li. = ligula, l.p. = labial palp, men. = mentum, mn. = mandible, m.p. = maxillary palp, p.g. = paraglossa, p.m. = prementum, p.n. = pronotum, s.m. = submentum.)

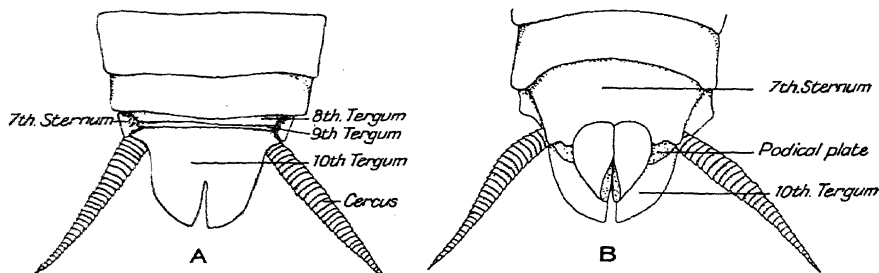


FIG. 157.—Posterior Abdominal Segments of female Cockroach (enlarged).

A, dorsal view; B, ventral view.

The abdomen consists of ten segments, each protected by a tergum and a sternum, which are joined to one another by thinner cuticular bands as in the thorax.

In the female cockroach (Fig. 157) only eight abdominal terga are clearly seen, the first seven and the tenth, the eighth and ninth

; concealed beneath the seventh. The tenth tergum is a broad flat plate, notched in the middle of its posterior margin, and beneath it are two triangular *podical plates*,¹ between which the anus is placed.

The abdomen of the male is, in general, like that of the female, save that it is more slender and has more convex terga, and attached to the sternum of the ninth segment are two short *anal styles*

beyond the edge of the tenth tergum of both sexes

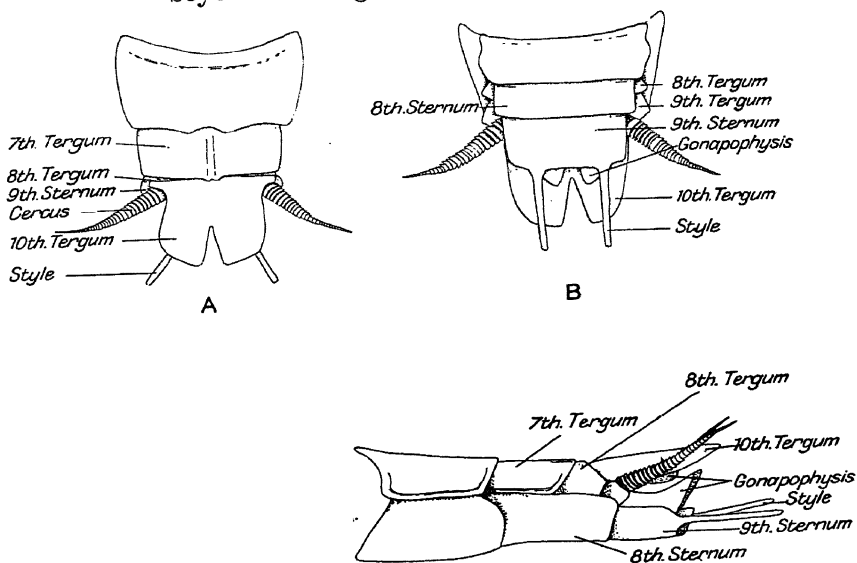


FIG. 158.—Posterior Abdominal Segments of male Cockroach (enlarged).

A, dorsal view; B, ventral view; C, lateral view.

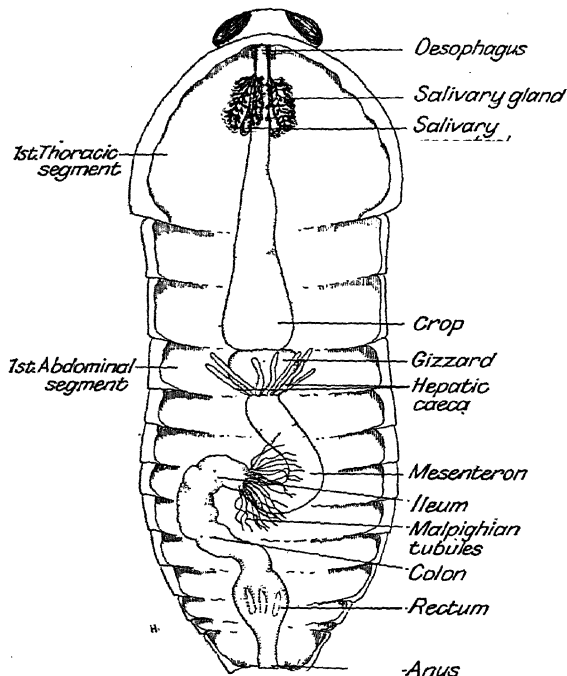
is a pair of jointed fusiform *anal cerci* which have been considered to be tactile or olfactory organs, although recent evidence suggests that they have an auditory function.

The genital opening is distinct from the anus and ventral to it, being provided with a series of chitinous plates and processes, the *gonapophyses*.

The Digestive System (Fig. 159). The digestive system consists of an elongated alimentary canal which is covered by a branched *fat-body*, which may play a part in nitrogenous excretion. It commences with the buccal cavity in the head, which is provided

¹ Sometimes considered to represent an eleventh abdominal segment.

with a muscular tongue-like outgrowth of the lower side, the *hypopharynx*, or *lingua*. Opening into the buccal cavity, on its ventral side, is the duct from the salivary glands situated at the anterior end of the thorax. From the buccal cavity a narrow *œsophagus* leads to a large thin-walled sac, the *crop*, which commences in the thorax but continues into the abdomen, where it becomes constricted posteriorly. Behind the crop is a short muscular *gizzard*, which is lined, in front, with chitinous projec-



159.—The digestive system of the Cockroach (*Periplaneta*), dorsal view [$\times 3$].

tions for mastication, and behind, with setæ, or bristles, for straining the broken food. The *mesenteron*, or *chylific stomach*, leads from the gizzard, receiving, at its anterior end, a series of about eight *hepatic cæca* which form a ring around it. A short narrow *ileum* continues from the mesenteron, and leads to a wider *colon* which ends with a swollen *rectum*, the lining of which is thrown into six longitudinal ridges. Leading into the anterior end of the ileum is a number of fine *Malpighian tubules* which are excretory organs ramifying in the fat-body, and the tracheal regions.

The cockroach is omnivorous as it will feed on almost any organic matter, not only eating the common foods found in houses, but also such things as hair, books, wall-paper, and the paste affixing paper to walls. On occasions it will consume a weaker fellow, leaving nothing but the chitinous exoskeleton.

The food, on entering the buccal cavity, comes into contact with the saliva which possibly contains a starch-digesting enzyme, although the main digestion occurs in the mesenteron, into which the hepatic cæca discharge a digestive fluid. The fluid of the hepatic cæca appears to resemble the pancreatic juice of the higher animals, for it is capable of digesting proteins, fats and carbohydrates. The soluble digested food is absorbed from the intestine and distributed to the tissues by the blood, undigestible matter being passed along and evacuated by the anus.

The excretory system of the cockroach consists of the Malpighian tubules, and perhaps the fat-body. The Malpighian tubules usually contain uric acid, and though equivalent to renal organs, do not possess distinct excretory apertures, but pass the nitrogenous waste matter into the ileum, from whence it is passed out with the fæces.

The Respiratory System. The respiratory system of the cockroach is typical of that of insects in general. It consists of a series of tubes, or *tracheæ*, which branch extensively in the body tissues to which they supply air.

The blood of the insect contains no hæmoglobin, and consequently takes little or no part in the carriage of oxygen to the tissues. As a result, the tracheæ must carry oxygen to and remove oxygen from the cells of the body. Air enters the system through ten pairs of small openings, the *spiracles*, situated laterally in the thorax and abdomen. The first two pairs of spiracles are situated between the prothorax and mesothorax, and mesothorax and metathorax respectively, whilst the other eight pairs are on the first eight abdominal segments. The tracheæ, leading from the spiracles, repeatedly branch to form finer *tracheoles* which ramify in the tissues. Air is introduced into the tracheoles, and expelled from them by movements of the abdominal muscles. The tracheæ have a chitinous lining, strengthened by fine spiral thickening, but the walls of the tracheoles are not so reinforced, and it is from this region that oxygen is removed from the air.

The Circulatory System. The vascular system of the insect resembles, in some respects, that of the earthworm, but is simplified in connection with the insect's mode of life. The blood is colourless, and consists of plasma containing leucocytes, but has no red cells or hæmoglobin. The *heart* takes the form of an elongated dorsal vessel, situated beneath the upper skin of the thorax and abdomen.

It is equivalent to the dorsal vessel of the earthworm, and is divided into thirteen chambers, corresponding to the segments of the body. Each chamber has a pair of lateral openings, or *ostia*, which communicate with a large blood space, or *hæmocœle*, surrounding the heart. The ostia are guarded by valves which allow blood to enter the heart from the hæmocœle, but do not permit it to pass in the reverse direction. From the heart an *anterior aorta* supplies blood to the head, but the remainder of the vascular system consists of an ill-defined series of spaces, or *sinuses*, in the tissues. The contraction of the heart forces blood forward to the head, and when the heart dilates, blood enters from the hæmocœle, into which the blood gradually drains from the various sinuses.

The blood is chiefly concerned with the carriage of food to the tissues, and the removal from them of soluble waste matter, the nitrogenous part of which is extracted by the fat-body and the Malpighian tubules.

The Nervous System (Fig. 160). The nervous system con-

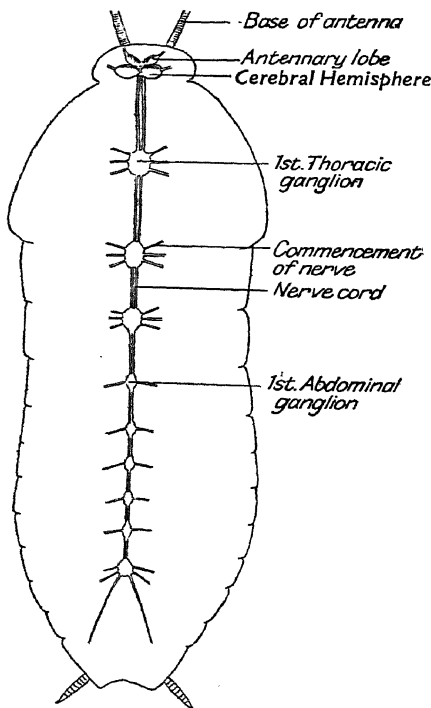


FIG. 160.—The nervous system of the Cockroach, from the dorsal side [$\times 3$].

sists of a *brain*, in the head, and a double nerve-cord running ventrally along the middle of the thorax and abdomen. The brain possesses two *cerebral hemispheres*, from which the optic nerves arise on each side the head, bearing on the front two smaller *antennary lobes* which send nerves to the antennæ. From the brain, two nerve-cords pass round the œsophagus and bear, below, the *sub-œsophageal ganglia* which unite, and supply nerves to the mouth. The nerve-cords pass backwards, bearing ganglia at intervals, the adjacent ganglia of each cord uniting. Three pairs of ganglia occur in the thorax and six pairs in the first six abdominal segments. The ganglia supply nerves to the segments in which they are situated, but the posterior pair supplies all the hinder segments of the body.

The sense organs associated with the nervous system include the compound eyes, the antennæ, the maxillæ, the anal cerci and various tactile hairs distributed over the body.

The eye (Fig. 161), is a complex structure composed of a series of

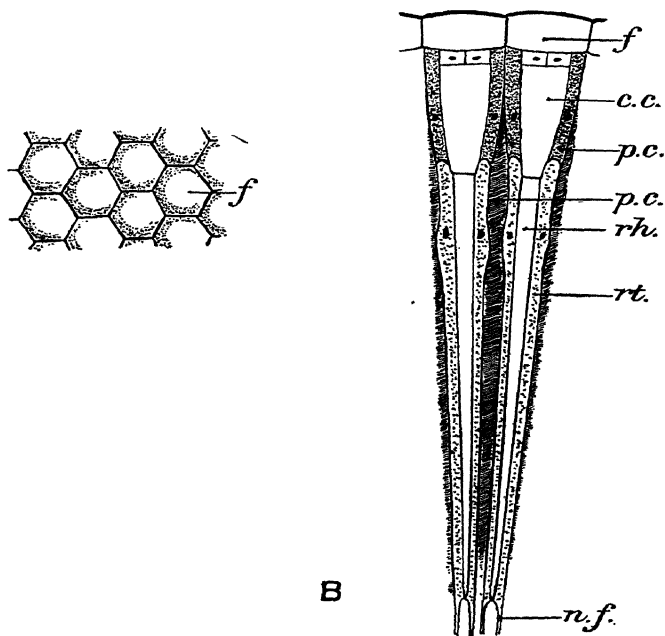


FIG. 161.—Compound Eye of an Arthropod.

A, part of eye in surface view; B, diagrammatic longitudinal section of two ommatidia.

: crystalline cone, *f* = corneal facet, *n.f.* = nerve fibre, *p.c.* = pigment cells, *r.h.* = rhabdome, *r.t.* = sensory cell of retinula.)

hexagonal units, or *ommatidia*, each of which has a *crystalline cone*, and the inner pointed end receives fibres from the optic nerve. Each ommatidium is covered on the outside by a transparent cuticular development, the *corneal facet*, or *lens*, which has, however, doubtful refractive powers. The ommatidia are separated from one another by black pigment cells which permit light to

netrate the cone from the facet only. Each unit of the eye is complete in itself, and as there are a large number in each eye it might be thought that the insect would receive the impression of many objects, when viewing one. This, however, is not the case, as the facet produces an image of what is immediately in front of it, and the impression is constructed from a series of partial images. The eye functions more as a warning organ than as a critical organ of vision, and the lateral position of the eyes on the head serves to record movements all around the insect.

The Reproductive System (Fig. 162). The reproductive system of both sexes is not acquired until after the final moult, so that it is not until this stage that the external differences between the male and female become apparent.

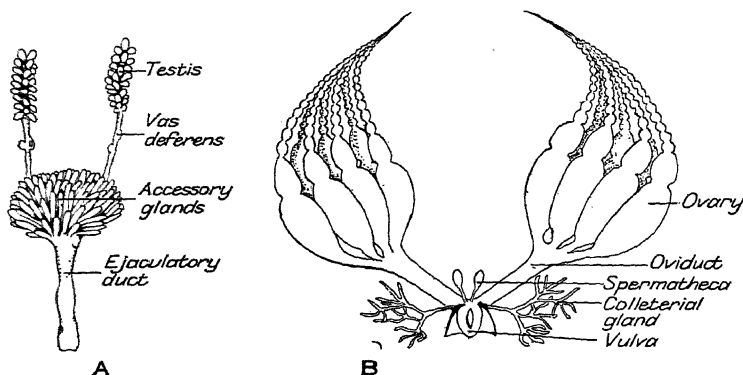


FIG. 162.—Reproductive Systems of the Cockroach.

A, male; B, female (much enlarged).

The male organs consist of a pair of *testes*, embedded in the fat-body below the terga of the fourth, fifth and sixth abdominal segments. Each testis is a chain of several nodules from which a *vas deferens* passes backwards to a median cluster of *vesiculæ seminales*. From the vesiculæ seminales an ejaculatory duct passes to the genital aperture, receiving, on its way, the duct of a

ventrally placed *conglobate gland*. The genital aperture is surrounded by chitinous gonapophyses, which articulate with those of the female during pairing.

The female organs are a pair of *ovaries* at the hinder end of the abdomen. Each ovary consists of eight processes which are pointed at the anterior distal end, the older eggs being found in the broader posterior part. Two short *oviducts* from the ovaries unite to form the vagina which opens by a slit-like aperture, the *vulva*, on the ventral side of the eighth segment.

Accessory to the female organs are the *spermathecae*, two small sacs, which open by narrow ducts on the ninth segment, and receive and store the spermatozoa deposited by the male during copulation. Immediately behind the openings of the spermathecae are the openings of a pair of much-branched *colleterial glands*, which secrete material to form the egg-capsule. Between the vulva and the anus are six symmetrically arranged gonapophyses, and the seventh sternum is prolonged backwards to form the concave floor of the *genital pouch*.

The deposition of eggs by the cockroach recalls that of the earthworm. Shortly after reaching maturity the male and female pair, the male depositing spermatozoa in the spermathecae of the female. A single deposition of spermatozoa suffices to effect the fertilisation of all the eggs laid during the life of the female, although the number of eggs laid may be considerable. After pairing, the female commences to lay eggs which travel down the oviducts from both ovaries into the genital pouch which has previously been lined with a secretion from the colleterial glands. When a number of eggs (from fourteen to twenty-eight) have been deposited, spermatozoa are shed over them from the spermathecae, and the egg-case, or *ootheca*, is completed around them. The ootheca is gradually extruded, and carried, for a short time, protruding from the hinder end of the female, from whence it is later deposited in a suitable place.

The fertilised eggs within the ootheca hatch in from three to six weeks, on which the ootheca cracks along the dorsal side to allow the young insects to emerge.

On emergence the young insects are small, and almost transparent, except for blackish eyes, but after moulting they soon acquire the characteristic dark colour. As the insect grows, further moults take place until the final development is completed.

During the developmental stage the antennæ or limbs may be injured or broken off, and the defect will persist until the next moult, when the part will be replaced, either wholly, or in part, according to the extent of the original injury.

The Mosquito (Fig. 163)

The mosquitoes and gnats are members of an order of typical insects, the Diptera. The mosquitoes are aquatic insects, and one of them, *Anopheles*, is of importance as the transmitter of malaria, a disease caused by a Protozoan parasite, described in Chapter XXVII.

The eggs are laid by the female *Anopheles* on the surface of still water, such as ponds, ditches and tanks. The eggs are concave, and possess air-sacs to enable them to float. They are laid singly, in contrast to those of another mosquito *Culex*, which form raft-like groups.

After several days, an aquatic larva hatches from the egg, being differentiated into head, thorax and an abdomen of nine segments. The larva lies parallel to and immediately below the surface of the water, and a pair of specialised spiracles on the eighth segment emerges through the water film to the atmosphere. The head is

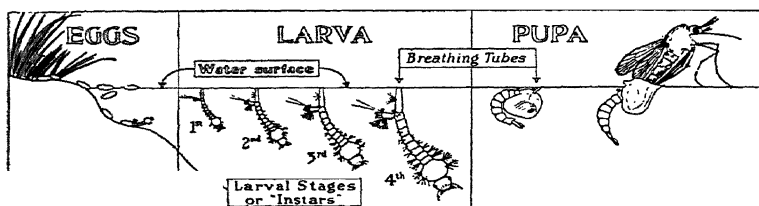


FIG. 163.—Stages in the life-history of a Culicine mosquito (*Aedes*). After Marshall.

provided with eyes, short antennæ, and strong biting jaws, by means of which the larva feeds on microscopic Algæ.

When disturbed, the larva sinks to the bottom of the pond, but soon returns to the surface, to resume its normal life. During the larval period, the insect sheds its skin several times, until, when fully grown, it becomes a curved pupa, or nymph, which can still move about, but does not feed. The nymph breathes by means of short projecting spiracles on the dorsal side of the thorax. At the end of the short pupal period, the insect emerges from the surface of the water, the thoracic skin splits dorsally and the adult insect escapes. The imago rests on the floating pupal skin until its wings have expanded, and its skin has hardened, on which it takes to flight.

The adult insect is about one centimetre in length and exhibits the usual characters of the class, viz. a body differentiated into head, thorax and abdomen, the thorax bearing three pairs of legs and the wings. The fore-wings only are fully developed as thin transparent

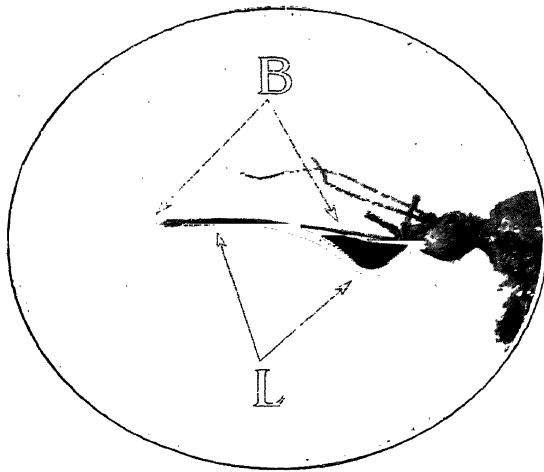


FIG. 164.—Head of a female mosquito showing the behaviour of the mouth during its insertion in the skin. The labium (*L*) bends as the other mouth-parts (*B*) puncture the skin ($\times 10$).



a. 182.—The effect of the thyroid gland on the growth of sheep. Both but that on the left had its thyroid gland removed. The sheep on the right is normal and acts as a control for comparison.

veined flight-wings, the hind-wings being small stalked swellings, the *halteres*. The head bears a pair of antennæ, provided with numerous bristles, and a pair of compound eyes. The mouth is composed of a series of chitinous segments, as in the cockroach, but in the mosquito the parts are modified to form a piercing, suctorial organ which is more complicated in the female. The labium forms a sheathing structure for the remaining parts, which, in the female, (a blood-sucking insect), consist of labrum-epipharynx, mandibles, maxillæ and hypopharynx, whilst in the male, which feeds on nectar and other vegetable juices, the mandibles are absent.

The female mosquito, which alone is the carrier of malarial parasites, feeds on the blood of man and other animals. It obtains the blood by placing the tip of the labium (which acts as a guide) against the skin of the victim, which is penetrated by the rest of the mouth, the labium bending as the other parts are inserted (Fig. 164). The mandibles and maxillæ produce the puncture; into which the hypopharynx carries a stream of saliva which prevents the blood from clotting and blocking the thin sucking tube formed by the combined labrum-epipharynx, and hypopharynx. The whole process occupies a minute or more, but once the skin has been penetrated infection by the mosquito can have taken place.

The usual carrier of malaria is *Anopheles maculipennis*, which is uncommon in Britain, but is occasionally present in some districts. If malarial subjects also occur in these regions there is always the possibility of the transmission of the disease to new human hosts, so that precautions should be taken to prevent the spread of the mosquito. Little can be done to control the adult insect, but it is possible to prevent the breeding of new generations. The simplest method of control consists in draining the areas in which the mosquito occurs, so that egg-laying will be prevented. Where drainage is not possible, the surface of the water should be sprayed with kerosene, or a similar oil, which lowers the surface-tension of the water so that it can no longer support the floating larvæ and pupæ, which consequently sink and die through lack of oxygen.

A common British mosquito is *Culex pipiens*, which rarely bites human beings, and does not harbour the malarial parasite. It may be distinguished from *Anopheles* by the fact that its larva is suspended head downwards from the surface of the water, and the imago rests with its body in a more or less horizontal position, in contrast to the adult *Anopheles* which rests with the hinder end of its body directed obliquely upwards.

CHAPTER XXV

CHORDATA. THE RABBIT

The rabbit is a member of the class Mammalia, belonging to the sub-phylum Vertebrata (= Craniata) of the phylum Chordata. The Mammalia also includes man, and such well-known animals as the dog, horse and cow. All mammals are characterised by the presence of hairs on the body (although in the whale, a marine mammal, the hairs occur only as bristles around the mouth), by the birth of living young, which undergo their early development within the body of the mother, and by the feeding of the young on milk, produced by the special *mammary glands* of the female. An important feature of mammals is that they are 'warm-blooded,' or *homoiothermic*, in which they contrast with all other Vertebrate groups (except the Birds), which are 'cold-blooded' or *poikilothermic*. Poikilothermic animals cannot regulate their body temperature, but must remain at about the same temperature as that of their surroundings. The mammals and birds maintain their body temperature more or less at a constant, no matter what the external conditions may be, the human body having a temperature of about 37° C., that of other mammals being one or two degrees higher. The advantage of a constant temperature lies in the fact that the metabolic processes, which involve enzyme activity, go on best at a certain optimum temperature. If the internal temperature of the body remains constant, the animal can carry out its normal activities at all times, whereas, if no temperature regulation is possible, the animal becomes less active at lower external temperatures, and more active with higher temperatures. This is evidenced by the natural hibernation of a 'cold-blooded' animal like the frog.

The internal heat of animals is obtained by the combustion of food during respiration. Heat is liberated in all living tissues, but particularly in active muscles, and is distributed through the body, largely through the agency of the blood-stream.

The more active are the muscles, the greater is the tendency towards a rise in body temperature, for the muscle cells use up their contained food to liberate energy, some of which is transformed to heat.

The skin of mammals (Fig. 130) is concerned in the regulation of body temperature, and in animals like the rabbit and the cat, which have a thick hairy covering of fur, this serves to retain heat within the body. The presence of fatty tissues beneath the skin is also a means of conserving heat, and those mammals, such as the seal and the polar bear, which are either aquatic, or inhabit colder parts of the world, possess abundant subcutaneous fat.

Under certain conditions, the temperature of the mammalian body may tend to rise, but this is prevented by the skin. When the body becomes overheated, the blood-vessels of the skin dilate and allow a greater amount of blood to be exposed close to the surface of the body, so permitting greater heat-loss to the atmosphere to occur. The flushing of the skin after vigorous exercise, which has caused a large liberation of heat within the body, or during hot weather, are instances of the behaviour of the blood-vessels of the skin. Another mechanism for preventing overheating is the *sweat-gland*, which is situated in the deeper layer, or derma, of the skin. Sweat-glands are distributed over the whole of the human body, but are less widely dispersed in other mammals, being localised particularly between the toes of the dog, cat and similar animals. The sweat-gland is a compact coiled tube, receiving a blood supply from the capillaries of the skin, and leads to the surface by a long duct, which excretes a watery fluid. As the excreted fluid evaporates from the skin surface, it causes a certain amount of cooling of the body to take place.

The Rabbit

The rabbit will serve as a representative mammal, and the details given apply to the mammalian body in general.

As the rabbit belongs to a particular order of mammals, the Rodentia, or gnawing-animals, it possesses the special dentition of that group, and as it is *herbivorous* its alimentary canal exhibits certain features connected with this habit.

General Characters.

The common rabbit (*Lepus cuniculus*) is found wild in many parts of Britain, where it excavates, or *burrows*, in suitable light soils. It is a timid animal, and during the daytime remains in the vicinity of its warren, to which it quickly retires when alarmed. It feeds on grasses, cereals, turnips, and other vegetable matter, and may gnaw the bark from the trunks or exposed roots of trees, so causing much damage in plantations. The rabbit is a source of food for several carnivorous animals such as foxes, stoats and various birds, which help to keep it in check, for it is a prolific breeder, often producing several litters of young each year.

The animal's body is covered externally with a dense fur of brownish colour, except on the underside of the tail, which is white. It consists of an elongated head, provided with a pair of large external ears, or *pinnae*, connected by a short neck to the trunk, which bears two pairs of limbs and terminates in a small tail.

The head possesses a rounded skull, flattened cheeks and an elongated face, on the under side of the anterior end of which is the mouth. The mouth is bounded by soft lips, the upper lip being divided in the middle so that the mouth is connected by grooves to the nostrils, which are two oblique slits at the end of the snout. The divided, or 'hare'-lip, found in the rabbit and related rodents enables the anterior gnawing-teeth to be applied closely to food material without causing injury to the lip.

The eyes are placed on either side the head, and are protected by upper and lower lids, and a *nictitating membrane*.

The snout bears a number of long hairs, the *vibrissæ*, or 'whiskers,' which are tactile, and similar hairs are found in the eye region.

On opening the mouth, the jaws bearing the teeth can be seen, and it will be noticed that there is a gap, the *diastema*, between the front, or *incisor* teeth and the grinding teeth at the back.

The trunk may be conveniently divided into two regions, an anterior *thorax*, protected ventrally by bony ribs, and a hinder *abdomen* which is soft and unprotected.

On the lower side of the thorax and abdomen of the female are two rows of *teats* which are the external parts of the milk-secreting, mammary glands, used when suckling the young. Teats also occur in the male, but they are small and undeveloped.

The *anus* opens immediately below the tail, and, in common with the majority of other Mammals, there is a separate urino-genital opening, ventral to it.

In the female, the urino-genital aperture is the *vulva*, which bears on its ventral wall, a small projection, the *clitoris*.

The male urino-genital aperture is borne at the end of a small protrusion, the *penis*, which can be withdrawn into a sheath of skin, the *prepuce*. At the base of the penis is a pouch, the *scrotum*, containing a pair of male organs, the testes.

Occurring in a slight depression on either side of the anus of both sexes is a bare patch into which opens the duct of the *perineal gland*, concerned with the secretion of a substance which gives the animal its characteristic odour.

The limbs are similar in construction to those of the frog, being built up on the pentadactyl plan. The fore-limbs are somewhat short and consist of upper arm, fore-arm and hand, or *manus*, which bears five digits. The hind-limbs are longer than the fore-

limbs, and consist of thigh, leg and foot, or *pes*, which possesses four digits. The digits of both sets of limbs are provided with horny *claws*, which are used in burrowing and for defence. The long hind-limbs are the main organs of locomotion, the rabbit usually progressing by a series of leaps.

The Skeletal System.

The skeleton of the rabbit is composed almost entirely of bone, cartilage being found only in the joints.

The skull is originally a cartilaginous structure, or *chondrocranium*, but, during the early development of the animal, this is replaced by bone. The adult skull consists of cartilage-bones, which originated as cartilage, and membrane-bones, which were

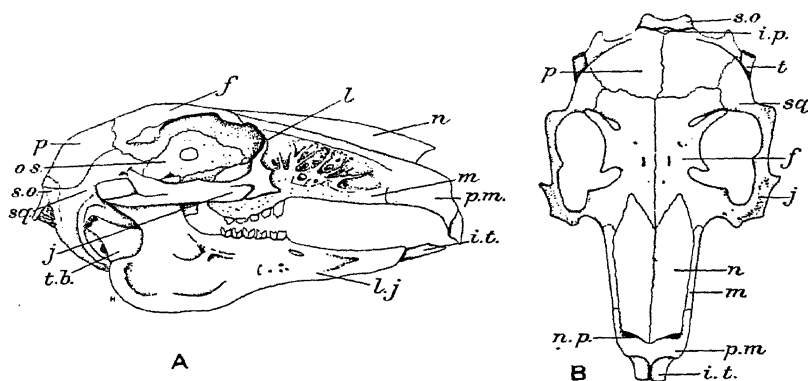


FIG. 165.—The skull of the Rabbit [$\times \frac{1}{2}$].

A, view from right side; B, view from above.

(*f* = frontal, *i.p.* = interparietal, *i.t.* = incisor teeth, *j* = jugal, *l* = lachrymal, *l.j.* = lower jaw, *n* = maxilla, *n.p.* = opening to nasal passage, *o.s.* = orbito-sphenoid, *p* = parietal, *p.m.* = premaxilla; *s.o.* = supra-occipital, *sq.* = squamosal, *t* = tympanic, *t.b.* = tympanic bone.)

laid down in connective tissue outside the chondrocranium, and the various bony plates articulate by irregular *sutures*. The bones of the skull were originally small, but expanded laterally as the animal grew. Between the various bones are small holes, or *foramina*, through which nerves and blood-vessels pass. In a few instances, foramina occur in the actual bone, which was formed around an existing nerve or blood-vessel. The various bones which form the skull are shown in Fig. 165, which should be studied along with an actual specimen.

The general composition of the rabbit's skull is not unlike that of the frog, as it consists of cranium, olfactory and otic capsules and upper and lower jaws.

The roof of the skull is formed in part by cranial bones, and in part by the nasal and otic capsules. The hinder end of the skull bears two rounded occipital condyles, which articulate with the first vertebra, and between them is the foramen magnum, a large opening through which the spinal cord emerges. The roof of the buccal cavity is a '*false palate*' formed by flat extensions of the *maxillæ* and *palatine bones* of each side, which meet in the middle line, *below* the true floor of the skull.

This results in the formation of a *nasal passage*, between the lower side of the skull and the '*false palate*,' the passage being divided vertically by a septum formed from the *mesethmoid bone*. The nasal passages also contain a number of spongy *turbinal bones*.

The upper jaw is formed by the *maxillæ* and *pre-maxillæ*, and the lower jaw by the *dentary bones*, which articulate with the *squamosals* of the upper part of the skull. The otic capsule is connected to the tympanic membrane of the middle ear by a chain of three small bones, the *auditory ossicles*, viz. innermost; lying against the fenestra ovalis is the perforated *stapes*, next to which is the *incus*, and outermost, the *malleus*, lying upon the tympanic membrane (Fig. 181).

The jaws of all mammals are provided with teeth, embedded

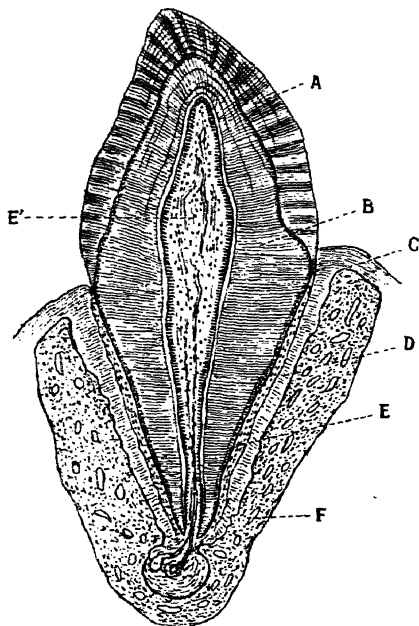


FIG. 166.—Longitudinal Section of a Mammalian Tooth.

(A = enamel, B = dentine, C = connective tissue, E = cement, E' = pulp, F = bone of jaw.)

in sockets, or *alveoli*, in the bone. The teeth of mammals are distinctive in form in different parts of the mouth, in contrast to the similarity of the teeth of other vertebrates. A typical tooth (Fig. 166) consists of a central *pulp*, outside of which is a hard *dentine* covered externally by a much harder *enamel*. The central pulp is provided with nerve fibres and blood-vessels which nourish the dentine-forming cells, or *odontoblasts*. Dentine is somewhat similar to bone in composition but has a different histological appearance. The enamel protects the inner tissues of the

tooth, so that if it is damaged decay soon follows. Most mammalian teeth grow to a mature size, and cease to enlarge, owing to the closing of the pulp-cavity in the formation of the '*roots*' of the tooth. Occasionally the pulp-cavity remains open and the growth of the tooth continues indefinitely. Such '*rootless*' teeth include the incisors of the rabbit, which elongate from within as the outer biting edges are worn away by friction of the teeth of the two jaws during use.

The teeth of mammals are replaced but once during the lifetime, in contrast to those of the lower Vertebrates which may be continually replaced. The first dentition consists of '*milk*' *teeth*, of which there are three kinds in the jaw, viz. *incisors*, *canines*, and *pre-molars*. The milk dentition is lost during the juvenile life of the animal and is replaced by the *permanent dentition*, which includes *molar teeth*, in addition to the three kinds of '*milk*' teeth. As a rule, there is a definite number of each type of tooth in the jaws of a particular mammal, the full complement of forty-four being found in the pig, other animals having certain teeth absent.

The tooth arrangement of a mammal is denoted by a *dental formula* in which are set down the initial letters of the teeth types followed by the number of such teeth present in the upper and lower jaws of *one* side of the mouth.

Thus, the dental formula of the pig is :

$$I_{\frac{3}{3}} \ C_{\frac{1}{1}} \ PM_{\frac{4}{4}} \ M_{\frac{3}{3}}$$

and that of man,

$$I_{\frac{2}{2}} \ C_{\frac{1}{1}} \ PM_{\frac{2}{2}} \ M_{\frac{3}{3}}$$

The rabbit has no canine teeth, a feature of all rodents, which gnaw, or crop, the food with their chisel-like incisor teeth, and pass it back along the diastema to the pre-molar and molar teeth for mastication. The dental formula of the rabbit is :

The vertebral column consists of a large number of vertebræ, articulated as to form a flexible support for the trunk and tail. Except in the sacral region, where they are fused together, the vertebræ are separated by cartilaginous *intervertebral discs*, which permit movement without transmitting shock. Five types of vertebræ (Figs. 167, 168), are present, classified on position as *cervical*, *thoracic*, *lumbar*, *sacral* and *caudal*, and there is usually a definite number of each kind in the backbone of a particular animal. The rabbit has seven cervical, twelve or thirteen thoracic, six or seven lumbar, three sacral, and about fifteen caudal vertebræ. Although all the vertebræ are constructed on the same

general plan, those of the various regions differ in distinctive details.

At the
the ge

from which arise laterally two thin outgrowths which use above the centrum to form the **neural arch** in which lies the spinal cord. Projecting dorsally from the neural arch is a bony **neural spine**, whilst on each side of the arch short **transverse processes** project. At the anterior and posterior ends of the arch

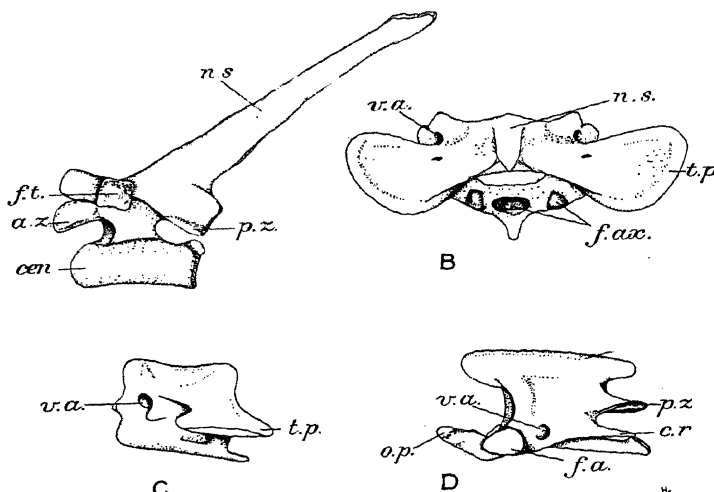


FIG. 167.—Vertebrae of the Rabbit [$\times 1\frac{1}{2}$].

A, thoracic vertebra, view of left side; B, atlas, dorsal view; C, the same, view of left side; D, axis, view of left side.

(a.z. = anterior zygapophysis (prezygapophysis), cen. = centrum, c.r. = cervical rib, f.a. = facet for articulation with atlas, f.a.x. = facet for articulation with axis, f.t. = facet for tuberculum of rib, n.s. = neural spine, o.p. = odontoid process, p.z. = posterior zygapophysis, t.p. = transverse process, v.a. = vertebral arterial canal.)

are pairs of processes, or **zygapophyses**, which bear facets for articulation with the adjacent vertebrae. The facets at the anterior end face upwards, and those of the posterior end downwards. Facets also occur on the sides of the centrum, a distinctive feature of thoracic vertebrae, for, together with the facets of the transverse processes, the central facets provide for the articulation of the ribs.

The cervical vertebrae (Fig. 168, A) are broader than those of the thoracic region, bearing no rib facets and having poorly developed neural spines. They possess, on each side, a small **vertebral arterial canal** in which the vertebral arteries pass. This canal is formed

by the fusion of small vestigial 'cervical ribs' with the transverse processes and centrum.

The first and second cervical vertebræ are modified in connection with the support of the head. The first, or *atlas* vertebra (Fig. 167, B, c), which has a ringlike form, has a reduced centrum and broad wing-like transverse processes to which certain head muscles are attached. At its anterior end are two sockets into which the occipital condyles of the skull fit, and the neural arch is divided by a ligament into two. Through the upper canal, so

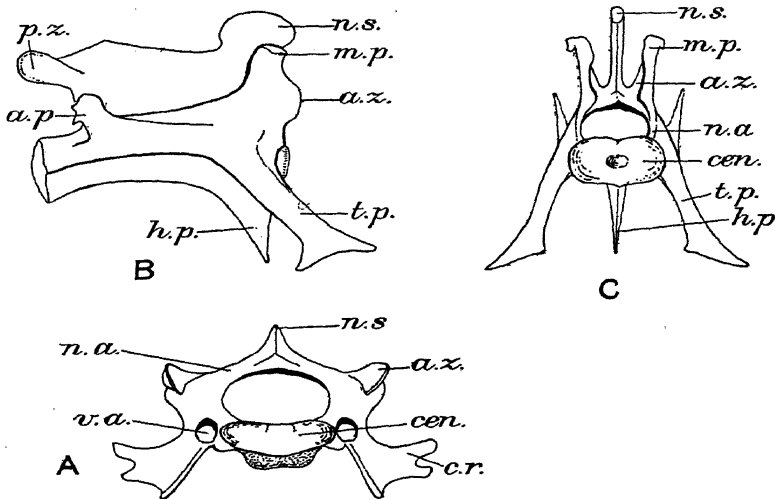


FIG. 168.—Vertebræ of the Rabbit [$\times 2$].

A, anterior view of a cervical vertebra; B, lumbar vertebra from right side; C, anterior view of the same.

(a.p. = anapophysis, h.p. = hypapophysis, m.p. = metapophysis, n.a. = neural arch. Other letters as for Fig. 167.)

formed, the spinal cord passes, whilst the lower cavity accommodates the *odontoid process* of the second vertebra. The second, or *axis* vertebra (Fig. 167, D) has a crest-like neural spine which projects anteriorly over the hinder part of the atlas. In front, its centrum bears the odontoid process which fits into the cavity provided in the atlas. The close association of the first two cervical vertebræ permits of head movements, the atlas allowing the head to move up and down, the axis enabling it to be turned. When the head is turning, the skull and the atlas are locked together, and make a combined movement, pivoting on the axis.

The lumbar vertebræ (Fig. 168, B) are large and strong as they

support the main part of the body. They possess large transverse processes, the neural spines project anteriorly, and additional outgrowths, the *metapophyses*, carry up the anterior zygapophyses. Posteriorly, small projecting *anapophyses* overhang the *intervertebral notches*, through which the nerves emerge from the spinal cord. The first and second lumbar vertebræ bear a median ventral *hypopophysis*.

The large sacral vertebræ are fused together, and bear lateral expansions for the support of the hip-girdle.

A certain number of the caudal vertebræ are fused to the sacral vertebræ to form the *sacrum* (Fig. 169), but the majority are free and become progressively reduced posteriorly, to mere bony cylinders supporting the tail.

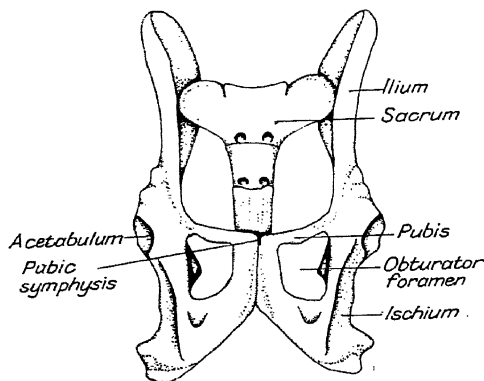


FIG. 169.—Pelvic girdle and sacrum of Rabbit (ventral view $\times \frac{3}{4}$).

The thorax is protected by the ribs and the breast-bone, or *sternum* (Fig. 170), which lies medially on the ventral side, and to which certain ribs are attached by *costal cartilages*. The rabbit has twelve pairs of ribs, seven of which are attached directly to the sternum. Of the remaining pairs, the eighth and ninth are united by cartilage to the seventh, but the last three pairs are free ventrally and are called '*floating ribs*.' Each rib possesses a curved *shaft*, and articulates with the thoracic vertebra by a *head* and a *tubercle*.

The sternum consists of seven segments, or *sternebræ*. The anterior sternebra projects forwards as the *manubrium*, the last expands posteriorly to form the *xiphisternum*, and the intermediate parts form the *mesosternum*.

The pectoral girdle is composed, on each side, of a dorsal trian-

gular *scapula*, or shoulder-blade, bearing on its upper border a cartilaginous *suprascapula*, and a slender *clavicle*, which curves ventrally towards the sternum, but is not attached to it. The apex of the scapula (Fig. 171) is directed forwards and downwards, and is hollowed ventrally to form the *glenoid cavity* in which the head of the humerus rests. At the side of the glenoid cavity is the

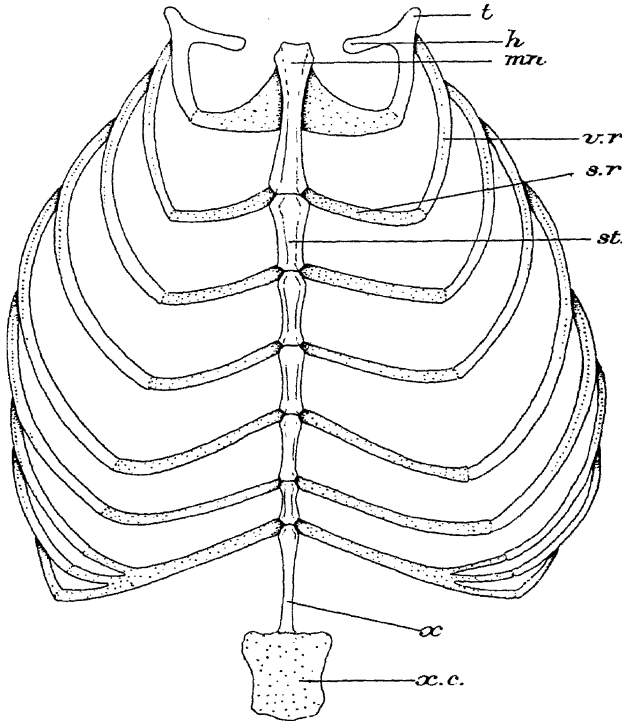


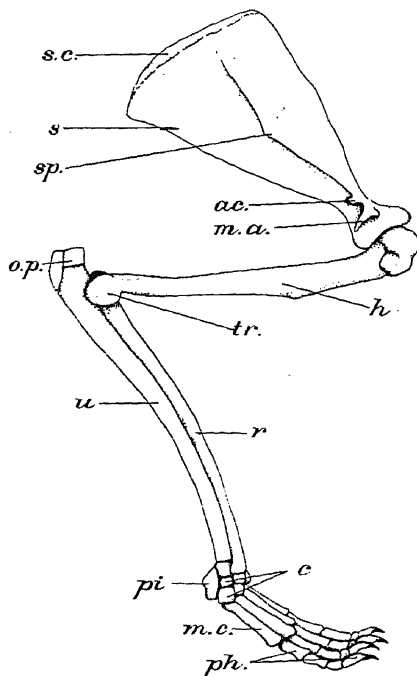
FIG. 170.—The breastbone and ribs of the Rabbit (ventral view $\times 1\frac{1}{2}$).

(*h* = head of rib, *mn.* = manubrium, *s.r.* = sternal portion of rib, *st.* = 2nd sternebra, *t* = tuberculum of rib, *v.r.* = vertebral portion of rib, which articulates dorsally with vertebral column, *x* = xiphisternum, *x.c.* = xiphoid cartilage.)

coracoid process. Along the outer surface of the scapula is a prominent ridge, which bears at its free end the *acromion* and *metacromion* processes.

The fore-limb, or arm, consists of the usual bones found in vertebrates (Fig. 171). The *humerus* is a long bone, with a columnar shaft, bearing, in front, the *deltoid ridge* for the attachment of the shoulder muscles. Its proximal, or inner, end is rounded and

fits into the glenoid cavity of the scapula, whilst its distal, or remote, end is a pulley-like *trochlea*, which articulates with the bones of the forearm to form the elbow-joint. Above the trochlea are two depressions, the *coronoid fossa* in front, and the *olecranon fossa* behind, both being involved in the movements of the elbow. The bones of the forearm are the *radius* and the *ulna*, the former being anterior, and the latter posterior and external. The radius is long



g. 171.—Right fore-leg, and scapula of Rabbit [$\times \frac{3}{4}$].

(ac. = acromion, c = carpals, h = humerus, m.a. = metacromion, m.c. = meta-carpals, o.p. = olecranon process, ph. = phalanges, pi. = pisiform bone, r = radius, s = scapula, s.c. = supra-scapula, sp. = scapular spine, tr. = trochlear, u = ulna.)

and slightly curved, its head being provided with two surfaces for articulation with the trochlea, and its distal end has a pair of shallow concavities for articulation with the carpal bones of the wrist. The ulna is longer than the radius, to which it is closely applied along its length. It articulates with the trochlea, but extends beyond it backwards as the *olecranon process*, which fits into the olecranon fossa of the humerus. The wrist consists of two rows of *carpal bones*, fitting closely together, and articulating with

the ends of the radius and ulna. There are three *proximal carpals*, known as the *scaphoid*, *semilunar* and *cuneiform* respectively, and corresponding to the radiale, intermedium and ulnare of the pentadactyl limb (Fig. 116). There is a small *centrale*, beyond which are four *distal carpals*, the *trapezium*, *trapezoid*, *magnum* and *unciform*, the last being a fusion of the fourth and fifth distal carpals. The hand possesses five *metacarpals* bearing the *phalanges* of the several digits. With the exception of the pre-axial digit, or thumb, which has two phalanges, the digits consist of three phalanges end to end. The terminal phalanx of each digit is enclosed in a horny claw, developed from the epidermis of the skin, and not, therefore, a true component of the endoskeleton.

The pelvic girdle articulates with the sacrum, the combined structure so formed being called the *pelvis* (Fig. 169). Each half of the pelvic girdle is called the *innominate bone*, although it consists of several bones, and the two halves are united ventrally by cartilage, the *pelvic symphysis*. The innominate, which is approximately parallel to the vertebral column, is composed of the *ilium*, which, after articulation with the sacrum, expands anteriorly and dorsally, the *ischium*, forming the dorsal posterior part of the innominate, and the *pubis*, forming the ventral part. About half-way along the outer surface of each innominate is a deep *acetabulum* into which the head of the femur fits. The skeleton of the hind-limb (Fig. 172) is very similar to that of the fore-limb. The *femur*, or thigh bone, has a prominent rounded head which fits into the acetabulum. It bears three irregular processes to which the leg muscles are attached, the *greater trochanter* to the outside, with the *third trochanter* below it, and the *lesser trochanter* to the inside. The distal end of the femur is slightly expanded to form two condyles which bear facets for the articulation of the tibia, and between them is the *patellar groove* which receives the *patella*, or knee-cap. The *tibia* and *fibula* of the leg are fused distally, but remain free at their proximal ends, where they articulate with the femur. The anterior side of the knee-joint is protected by the patella, a small bone, known as a *sesamoid*, as it originates in the ligament which connects muscles to the tibia. The patella prevents injury to the tendons which lie across the knee-joint when the limb is extended. In the ankle the *tarsal bones* are arranged in two rows like the carpals of the wrist. The *proximal tarsals*, articulating with the fused tibia-fibula, are two in number, viz. the *astragalus*, lying on the inner side, and representing the fused tibiale and intermedium of the primitive pentadactyl limb, and the *calcaneum* (= radiale) which is produced backwards to form the heel. The centrale, or *navicular*, lies in front of the astragalus.

There are three *distal tarsals*, one being a fusion of the fourth and fifth of the primitive limb, whilst the first is absent, together with the digit it would have borne. The second distal tarsal is called the

hind, the *ectocuneif*
fourth and fifth, the *cuboid*. The foot possesses four digits, each with three phalanges, as in the hand, the terminal phalanges are invested with claws

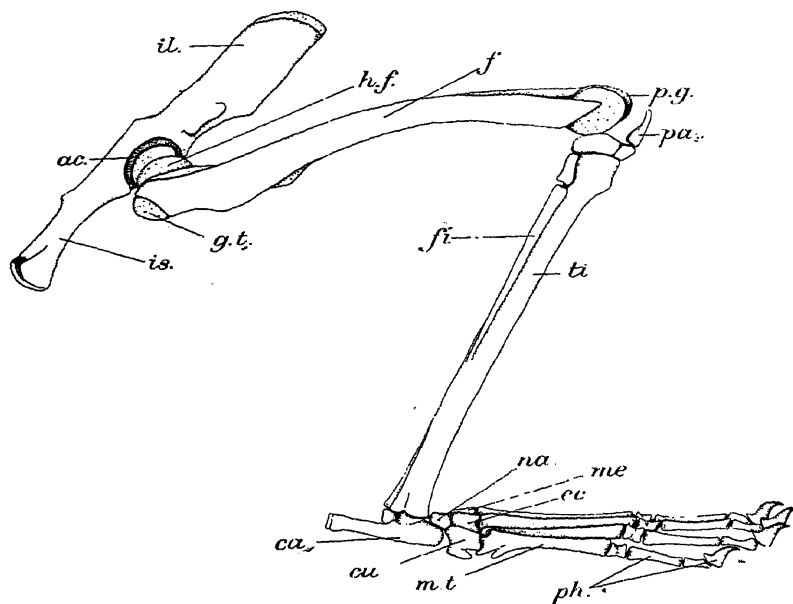


FIG. 172.—Skeleton of the right hind-limb, and hip-girdle of the Rabbit
[$\times \frac{3}{2}$].

(ac. = acetabulum ca. = calcaneum (fibulare), cu. = cuboid, ec. = ectocuneiform, f. = femur, fi. = fibula, g.t. = great trochanter, h.f. = head of femur, il. = ilium, is. = ischium, me. = mesocuneiform, m.t. = metatarsal, na. = navicular (centrale), pa. = patella, p.g. = patellar groove, ph. = phalanges, ti. = tibia.)

The limb-joints possess greater powers of movement than are met elsewhere in the skeleton, and in the joints the ends of opposing bones remain cartilaginous and enclose between them a *synovial capsule*, lined with a membrane secreting a synovial fluid which acts as a lubricant.

Internal Structure (Fig. 173).

The general internal structure of the rabbit can be examined by dissecting the animal from the ventral aspect, after removing the

skin, which is attached to the muscular body-wall by a loose areolar connective tissue, or superficial fascia.

The arrangement of the viscera resembles that of the frog, but a feature of difference, distinctive of the mammals in general, is that the coelom is divided transversely by a convex muscular partition,

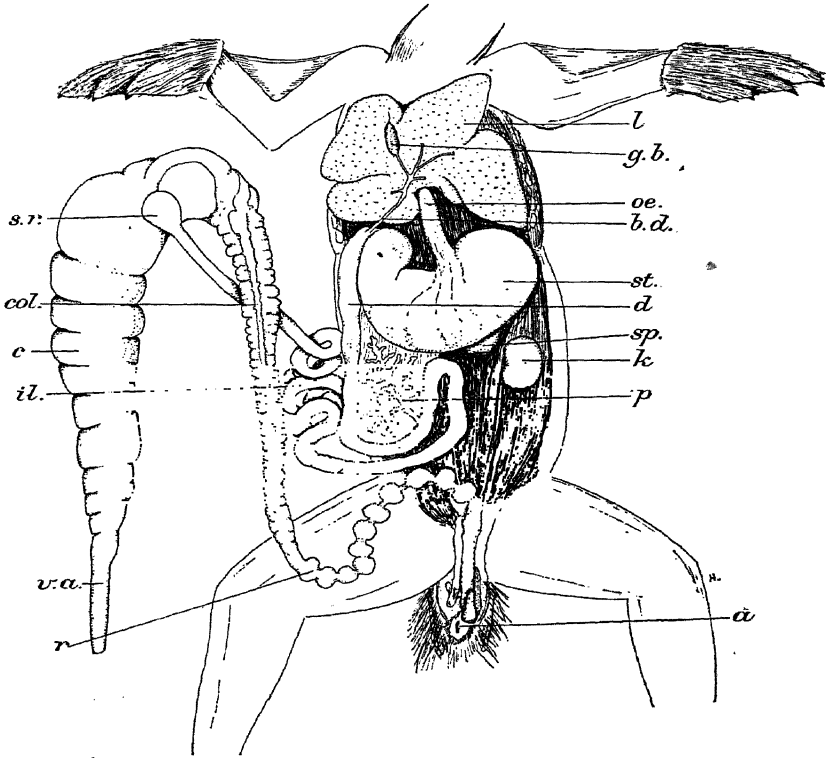


FIG. 173.—The Rabbit (*Lepus cuniculus*).

Dissection to show the alimentary system from the ventral aspect. (Part of the system has been displaced.)

(a = anus, b.d. = bile duct, c = caecum, col. = colon, d = duodenum, g.b. = gall bladder, il. = ileum, k = kidney, l = liver, oe. = oesophagus, p = pancreas, r = rectum, containing faecal pellets, sp. = spleen, s.r. = sacculus rotundus, st. = stomach, v.a. = vermiform appendix.)

the **diaphragm**, below the ribs. The coelom consists, therefore, of an anterior thoracic cavity and a posterior, abdominal, or peritoneal cavity. The thorax contains the lungs which are enclosed in **pleural cavities**, formed by a double-membrane, the **pleura**, which covers the lungs, and externally is applied to the lining of the

thorax. The inner walls of the pleural cavities of the two lungs enclose a dorsi-ventral lymph space, the *mediastinum*, in the ventral part of which lies the heart, enclosed in a *pericardial cavity*. The abdominal cavity contains the remaining viscera including the stomach, liver, pancreas, intestines, spleen, bladder and the reproductive organs. As in the frog, the kidneys are situated immediately outside the back of the coelom, from which they are separated by a thin transparent membrane.

The diaphragm is pierced by the alimentary canal and various blood-vessels.

The Digestive System (Fig. 173).

The alimentary canal commences with the buccal cavity, the roof of which is formed by the false-palate. The anterior part of the false-palate is bony and is known as the *hard-palate*, but at the back of the mouth it is devoid of bone, and known as the *soft-palate*, behind which the nasal passages open. Attached to the hinder end of the floor of the cavity is a large fleshy tongue which bears, at the back, a lateral pair of *papillæ foliatæ*, particularly concerned with the perception of taste, although *taste-buds* are also dispersed over the rest of the tongue, on the soft-palate and elsewhere in the mouth. The Eustachian tubes open into the buccal cavity near the internal openings of the nasal passages. The soft-palate ends behind in a median *uvula* and an arch, bearing the *tonsils* on its sides, leading to the pharynx. The pharynx leads, above, to the oesophagus, and below, to the *trachea*, or windpipe. The entrance to the trachea is protected by an elastic projection, the *epiglottis*, which closes the tracheal opening when food is passed into the oesophagus. The teeth, which are an integral part of the alimentary system, have already been considered. Entering the buccal cavity are the ducts of four pairs of *salivary glands*, two pairs being associated with each jaw. The *parotid glands* lie in front of the ears, the *infraorbital glands* are below and anterior to the eyes, the *submaxillary glands* lie on the inner side of the angle of the jaws, and the *sub-lingual glands* are on either side the tongue, on the inner side of the lower jaw. These glands secrete the *saliva*, a juice containing mucus and the enzyme ptyalin, which are mixed with the food during mastication.

From the buccal cavity, the oesophagus passes down the neck, through the thorax and penetrates the diaphragm to reach the stomach. The stomach lies transversely in the abdomen and consists of a broad cardiac portion which receives the oesophagus, and a narrow pyloric end which is closed by a circular band of smooth muscle, the pyloric sphincter. Beyond the pylorus is the much-convoluted small intestine, some 6 feet in length, which :

be resolved into two regions, the duodenum and the ileum. The duodenum is the upper loop, which, close to the stomach, receives the bile-duct from the gall-bladder, and, lower down, the pancreatic duct. The two ducts enter independently in the rabbit, in contrast to their common entry into the intestine of the frog. The liver is a large dark red organ lying against the diaphragm and fitting closely around the stomach. It consists of right and left lobes, which are further subdivided, and between them is the oval green gall-bladder. The pancreas of the rabbit is an ill-defined organ, consisting of a mass of tissue suspended in the mesentery supporting the two limbs of the duodenum. The lining of the small intestine is a mucous membrane drawn out into numerous contractile papillæ, the *villi*, which greatly increase the area of the lumen. The mucous membrane of both stomach and small intestine bear glands concerned in the secretion of digestive fluids.

The lining of the ileum bears islands of lymphoid tissue known as *Peyer's patches*, from which lymphocytes may enter the alimentary canal.

The ileum ends in a small dilatation, the *sacculus rotundus*, also having lymphoid tissue in its walls, and from this the *cæcum* and large intestine pass. The cæcum of the rabbit, and some other herbivorous animals, is well-developed, being a wide tube with a spiral constriction, ending blindly as a thick-walled *vermiform appendix*. It is believed that in the cæcum, cellulosic material of the vegetable food is broken down by bacteria and thus made available to the animal. The lining of the vermiform appendix contains much lymphoid tissue and may be important as a phagocytic organ.

The large intestine, or *colon*, is a muscular tube having an annulated appearance at its commencement, but becoming smooth-walled lower down. The colon leads to the rectum, which usually has a nodulated appearance owing to the presence of faecal pellets which pass down it to the anus.

The digestive processes commence in the buccal cavity where the food is masticated by the pre-molar and molar teeth, and mixed with the saliva. The ptyalin of the saliva acts on starchy matter to form maltose, whilst the mucus of the saliva moistens and lubricates the food for its passage down the oesophagus. A bolus of food is swallowed, and by *peristalsis*, or muscular waves in the wall of the oesophagus, it passes to the stomach, where it is mixed with the gastric juice, by the contraction and relaxation of the stomach-wall, particularly towards the pyloric end. The pepsin of the gastric juice, assisted by the hydrochloric acid secreted by special cells of the stomach-wall, acts on proteins, as in the frog's stomach. The

food gradually becomes more fluid, and, as chyme, is periodically passed into the small intestine by the relaxation of the pyloric sphincter. In the small intestine the food comes in contact with bile, pancreatic juice and the succus entericus. The bile assists in the emulsification of fats, assisted by the alkaline nature of the intestinal secretions. The pancreatic juice and the succus entericus contain enzymes, which act on the foods which have not so far been digested, in the same way as was described on p. 236.

The main digestive processes occur in the small intestine and it is from here that soluble food is absorbed. Sugars and amino-acids enter the blood-vessels of the villi which pass them to the liver by the portal vein. Simplified fats are passed from the intestine into the lacteals of the villi where the fats are re-formed and carried to various tissues to be stored.

In the liver glucose is transformed to glycogen for temporary storage, being reconverted to glucose and circulated in the blood later, as required by the body. Of the amino-acids passed to the liver, some are passed on directly to the tissues for growth and repair, but others are deaminised, in which ammonia is split off, which may form urea ($\text{CO}(\text{NH}_2)_2$), excreted, in due course, in the urine.

Although the food of the rabbit includes a large proportion of cellulose, none of the digestive juices appears to contain the enzyme cellulase, necessary for its digestion. As the cæcum contains numerous bacteria possessing cellulase, it is possible that their activities render some of the cellulose, passed down the intestine, available to the animal.

The undigested residue of the food which passes to the colon is deprived of most of its water, which is absorbed by the wall. The more solid faeces continue to the rectum to be evacuated in the form of pellets.

The Circulatory System (Fig. 174).

The circulatory system of the rabbit is, in many respects, like that of the frog, but is more efficient, as venous and arterial blood are separated completely during circulation. The blood of mammals has been described on p. 258, and that of the rabbit is of this type, the red blood cells being 0.0065 millimetre in diameter.

The spleen is a large red organ lying in the mesentery close to the stomach. It acts as a reservoir for red blood cells, which may be passed into circulation according to the needs of the body. The red marrow, found in the cavities of the long bones, is concerned with the manufacture of red blood cells, and certain forms of leucocyte, other leucocytes being formed in lymphoid tissues.

The mammalian heart can be studied in that of the sheep, which,

owing to its size, displays the features satisfactorily. In all respects the rabbit's heart is similar, and the description given below applies to it.

The heart (Fig. 175) lies in the middle of the thorax in the medias-

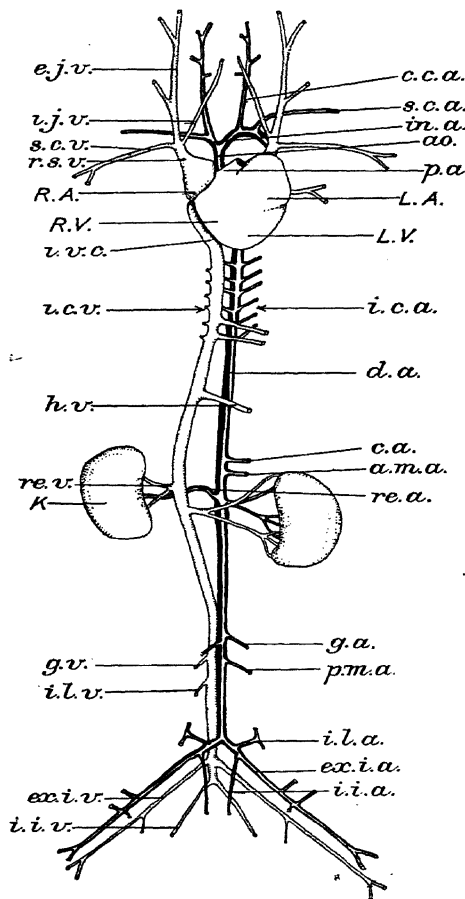


FIG. 174.—The Circulatory System of the Rabbit—diagrammatic ventral view. (Venous System—white, Arterial System—black.)

(*a.m.a.* = anterior mesenteric artery, *a.o.* = aorta, *c.a.* = coeliac artery, *c.c.a.* = common carotid artery, *d.a.* = dorsal aorta, *e.j.v.* = external jugular vein, *ex.i.a.* = external iliac (femoral) artery, *ex.i.v.* = external iliac vein, *g.a.* = genital artery, *g.v.* = genital vein, *h.v.* = hepatic vein, *i.c.a.* = intercostal artery, *i.c.v.* = intercostal vein, *i.i.a.* = internal iliac artery, *i.i.v.* = internal iliac vein, *i.j.v.* = internal jugular vein, *i.l.a.* = ilio-lumbar artery, *i.l.v.* = ilio-lumbar vein, *in.a.* = innominate artery, *i.v.c.* = inferior vena cava, *K* = kidney, *L.A.* = left auricle, *L.V.* = left ventricle, *p.a.* = pulmonary artery, *p.m.a.* = posterior mesenteric artery, *R.A.* = right auricle, *re.a.* = renal artery, *re.v.* = renal vein, *r.s.v.* = right superior vena cava, *R.V.* = right ventricle, *s.c.a.* = subclavian artery, *s.c.v.* = subclavian vein.)

tinal space between the lungs. It is enveloped by a thin *pericardium* of two layers, forming a pericardial cavity containing fluid. The heart consists of two thin-walled auricles, below which are two thick-walled ventricles, the wall of the left ventricle being somewhat more muscular than that of the right ventricle. Blood-vessels enter and leave the various chambers of the heart, and the right and left sides are completely separated by a median septum. The auricle and ventricle, of each side of the heart, are separated by a transverse septum provided with valves, permitting blood to flow from auricle to ventricle, but preventing any reflux. Between the right auricle and ventricle is the *tricuspid valve*, consisting of three flaps, fastened by *chordæ tendineæ* to projecting *papillary*

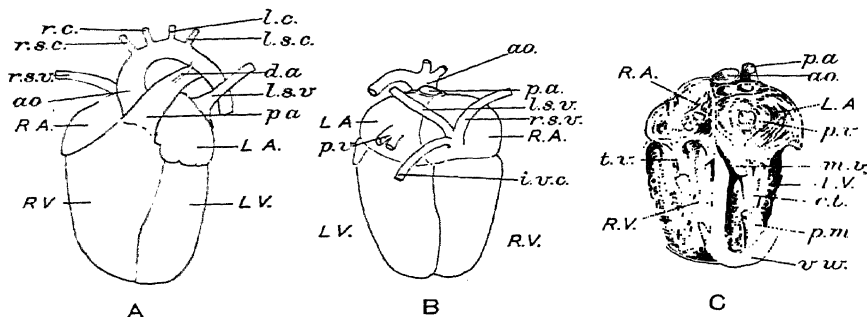


FIG. 175.—The heart of the Rabbit [$\times \frac{3}{2}$].

A, ventral view; B, dorsal view; C, longitudinal section through both auricles and ventricles.

(*ao.* = aorta, *c.t.* = chorda tendinea, *d.a.* = ductus arteriosus, *i.v.c.* = inferior vena cava, *L.A.* = left auricle, *l.c.* = left common carotid artery, *l.s.c.* = left subclavian artery, *l.s.v.* = left superior vena cava, *L.V.* = left ventricle, *m.v.* = mitral valve, *p.a.* = pulmonary artery, *p.m.* = papillary muscle, *p.v.* = pulmonary veins, *R.A.* = right auricle, *r.c.* = right common carotid artery, *r.s.c.* = right subclavian artery, *r.s.v.* = right superior vena cava, *R.V.* = right ventricle, *t.v.* = tricuspid valve, *v.w.* = wall of left ventricle.)

muscles of the ventricle wall. Between the left auricle and ventricle is the *mitral valve*, consisting of two flaps, attached in the same manner as the tricuspid valve to the ventricle wall.

Entering the right auricle are three venæ cavæ, returning blood from all parts of the body, and, leaving the right ventricle, is a large pulmonary artery which carries the reduced venous blood to the lungs.

The pulmonary veins, carrying oxygenated blood from the lungs, unite and enter the left auricle, whilst ascending from the left ventricle is the large *aorta*, which distributes the arterial blood to the body.

The exits of the aorta and the pulmonary artery from the heart are each guarded by three *semilunar valves* which permit blood

to flow from the heart only. The arteries and veins mostly follow the same general course in the body, but exceptions are found in the behaviour of certain large vessels and those of the portal system.

The arterial system commences with the aorta, which ascends from the left ventricle but soon curves backwards and downwards on the left side, giving off various branches as it continues on its course through the trunk as the *dorsal aorta*. The first anterior branch of the aorta is the short *innominate artery* which branches almost immediately to form the *right subclavian artery* and the *right common carotid artery*. The right subclavian gives off a *vertebral artery* to the back, and an *internal mammary artery* to the chest, and proceeds, as the *brachial artery*, to supply the right fore-limb. The right common carotid runs up the neck, and divides near the angle of the jaw to form the *right internal* and *external carotid arteries*, the former supplying the skull, and the latter the face. As the aorta bends to the left it gives off the *left common carotid artery*¹ and the *left subclavian artery*, both with a distribution on the left of the body similar to that of the corresponding arteries on the right. On reaching the dorsal side of the heart the aorta sends a number of pairs of *intercostal arteries* to the thoracic wall, and, immediately on passing through the diaphragm, sends to it a pair of *phrenic arteries*.

In the abdomen the aorta continues along the dorsal wall, ventral to the spinal column, and gives off three single arteries which are carried in the mesentery to the alimentary canal and its accessory parts. The *coeliac artery* supplies the liver, stomach and spleen, branching to form the *hepatic artery* to the liver, and the *lienogastric artery* to the two other organs. The *anterior mesenteric artery* passes to the intestines and the pancreas, and the *posterior mesenteric artery* passes to the rectum. In addition to these unpaired vessels, the aorta distributes pairs of arteries to the paired organs of the abdomen. Between the anterior and posterior mesenteric arteries are the *right and left renal arteries* to the kidneys (the right arising slightly anterior to the left) and the *genital arteries* to the reproductive organs. In the female, the genital arteries are called *ovarian arteries*, and in the male they are *spermatic arteries*. The spermatic arteries of the adult male are long as they pass down the abdomen in the spermatic cord to the testes contained in the scrotum. This elongation of the spermatic arteries is due to the fact that the testes originate in the abdomen close to the kidneys, but descend to the scrotum as the animal reaches maturity.

Below the posterior mesenteric artery the aorta branches to the

¹ Occasionally this artery is a branch of the innominate.

right and left to form a pair of *common iliac arteries* to the hind-limbs and the back, but just before division it sends a small median *caudal artery* to the tail. In the abdomen the common iliacs each give off an *ilio-lumbar artery* to the dorsal hinder part of the abdomen, and an *internal iliac artery* to the anal region, and on entering the limbs become the *femoral arteries*.

As in the frog, the arteries divide into small arterioles which branch to form narrow capillaries in the tissues to which blood is distributed. The capillaries join up again to form venules which ultimately join together to form the larger veins which return the blood to the heart.

The blood from the head is returned, on each side, by the *external* and *internal jugular veins*. The external jugular runs towards the outside of the neck, being formed by the union of the *posterior facial vein* from the ear, and the *anterior facial vein* from the face. The internal jugular is a smaller vein running parallel to the trachea and drains blood from the region of the brain. From the fore-limbs the *brachial veins* enter on each side, and after receiving smaller veins from the shoulders are known as the *subclavian veins*, which unite with the jugular veins of each side and pass into the right auricle, independently, as the *right* and *left superior venæ cavæ*. On the right, there is an additional *azygos vein*, which returns blood from the thorax and enters the right superior vena cava close to the auricle. The blood from the hind-limbs returns by the *internal iliac veins* and the *femoral* (or *external iliac*) veins which unite to form the *inferior vena cava* which runs upwards to the heart in the middle line. On its way to the right auricle the inferior vena cava receives, in turn, a pair of *ilio-lumbar veins* from the back, a pair of *genital* (*ovarian* or *spermatic*) *veins* from the reproductive organs, a pair of renal veins from the kidneys, and the *hepatic veins* from the liver.

The circulatory system so far described is known as the *systemic circulation*, but in addition there are three other systems.

The *pulmonary circulation* consists of the large pulmonary artery, which leaves the right ventricle and branches to carry deoxygenated *venous* blood to the lungs and the pulmonary veins, which return from the lungs with oxygenated *arterial* blood and enter the left auricle together.

In the adult rabbit a thin cord the *ductus arteriosus*, joins the left pulmonary artery to the aorta. In the embryo this structure is a true blood-vessel, but becomes blocked up during the later development of the vascular system.

The *portal circulation* is an important system concerned with the conveyance of blood, containing food absorbed from the intes-

tine, to the liver. From the stomach and spleen comes the *lienogastric vein*, from the duodenum, the *duodenal vein*, from the lower part of the small intestine, the *anterior mesenteric vein*, and from the rectum, the *posterior mesenteric vein*. These veins unite in various ways to form a large *portal vein*, which enters the liver lobes by several branches, and distributes blood to the liver cells. The blood is re-collected into the hepatic veins and passed to the inferior vena cava.

In mammals there is a special circulatory system supplying the muscular wall of the heart. This is the *coronary circulation* which commences with two *coronary arteries* which emerge from the aorta immediately outside its semi-lunar valves. The coronary arteries branch in the heart-wall, and form a capillary system ramifying amongst the muscle fibres. The blood is mainly returned to the right auricle by *coronary veins*. It may be noted here that the frog's heart does not possess coronary arteries, but some blood may pass into the spongy ventricle wall from the ventricular cavity.

The circulation of blood in the rabbit is maintained, as in the frog, by rhythmic contraction and relaxation of the heart.

The cardiac cycle is initiated in the junction between the venæ cavæ and the auricle. It commences with a contraction of the auricles followed by a contraction of the ventricles, and ends with a relaxation of both auricles and ventricles.

The right auricle contains deoxygenated (venous) blood received from the body, whilst the left auricle receives oxygenated arterial blood from the lungs. On the simultaneous contraction of the auricles, the contained blood is passed to the respective ventricles, which on contraction expel the blood from the heart. Thus deoxygenated blood leaves the right ventricle by the pulmonary artery, which carries it to the lungs, and oxygenated blood flows to the body from the left ventricle, by way of the aorta.

The flow of blood in one direction is maintained by the various valves of the heart and its arteries. The entry of blood into the coronary arteries takes place as the ventricle relaxes, for it is at this stage that the muscular wall offers least resistance to the flow of blood through it.

The rabbit possesses a lymphatic system which collects up the tissue fluid which has filtered from the blood. It consists of a complicated series of vessels which are not only concerned with the carriage of lymph, but, in the mesentery, carry a large part of the fat absorbed by the lacteals in the villi of the small intestine. The central vessel of the system is a large *thoracic duct* which connects with the left superior vena cava close to the subclavian vein.

The Respiratory System.

The rabbit is an air-breather, and its respiratory organs are the lungs, with which are associated the trachea and its branches, and the nasal passages. The nasal passages, situated above the false-palate, are lined with a ciliated mucous membrane which is kept moist and warm. As air passes along the passages it is warmed and filtered in its prolonged path necessitated by the presence of the turbinal bones. The nasal passages open into the pharynx close to the glottis, through which the air enters the trachea. At the anterior end of the trachea is a short larynx concerned with the emission of sound. Both the trachea and larynx are supported by rings of cartilage which prevent their collapse. The trachea passes down the neck in front of the oesophagus, and in the thorax divides into right and left *bronchi* which pass to the two lungs. Each lung consists of several lobes, supplied with a *bronchiole* (or branch of the bronchus), and the lungs are enclosed in the pleural sacs. The intimate structure of the lung consists of small air-sacs, or *infundibula*, divided up into smaller sacs, the alveoli, in which the gaseous exchanges between the blood and the air take place. Each alveolus is lined with a thin squamous epithelium, and its wall contains numerous capillaries which readily permit the gaseous exchanges between blood and air.

The breathing of mammals consists of the inflation and deflation of the lungs which involve the action of the ribs and the diaphragm. During inspiration, the ribs rise and the diaphragm falls, so causing an increase in the volume of the thorax. As the pleuræ are in close contact with the lining of the thorax, an increased negative pressure occurs, which causes air to be drawn into the lungs, through the nasal passages, trachea and bronchi. Expiration is brought about by a lowering of the ribs and the rise of the diaphragm, assisted by the recovery of elastic fibres in the lung wall, which were stretched during inflation. All these factors serve to collapse the lung partially and expel the air.

In breathing, there is never a complete emptying and refilling of the lungs, for a considerable volume of air remains in the alveoli at the end of each expiration and the gaseous exchanges with the atmosphere are relatively small. The amount of air exchanged in each inspiration and expiration is called the *tidal air*, which diffuses into the air which has remained in the alveoli.

The carriage of the gases to and from the tissues is exactly similar to what has been previously detailed for the frog.

The Urino-genital System (Figs. 176, 177).

The excretory organs consist of two dark red kidneys situated slightly asymmetrically near the middle line at the back of the

abdomen, being separated from the coelom by a thin peritoneal membrane. The kidney is of characteristic shape, and from the middle of its curved side, at a point called the *hilum*, the ureter and renal vein emerge, and the renal artery enters. The kidney tissue consists of an outer *cortex* and an inner *medulla*, the uriniferous tubules arising in the former. Each tubule is essentially the same as that of the frog, consisting of a capsule surrounding a glomerulus, and ducts leading to the ureter. From the kidneys the ureters run backwards to the urinary bladder in which the excreted urine is collected.

From the bladder of the male a urethra leads through the penis to the urino-genital aperture at its apex, but in the female the broad urethra opens into the vulva.

The function of the kidney is to remove soluble waste material, including urea, from the blood-stream. The blood which enters the kidney by the renal artery passes to the glomerulus by an *afferent glomerular arteriole*. Fluid passes from the blood into the capsule of the tubule, and the remaining blood leaves the glomerulus by an *efferent arteriole* and ultimately reaches the renal vein for return to the heart. The fluid in the tubule, known as the *glomerular filtrate*, passes along, to the ureter, but on its way some reabsorption of water and other substances occurs before it is excreted as urine.

The reproductive system, in common with that of all vertebrates, is associated with the excretory system.

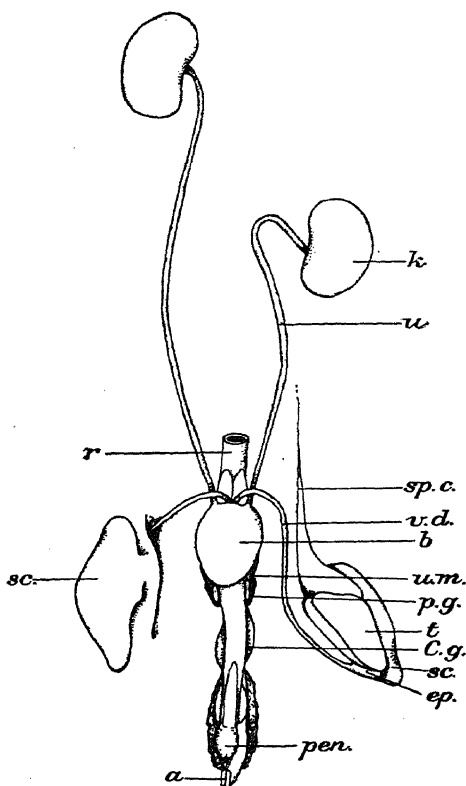


FIG. 176.—Urino-genital System of the male Rabbit (ventral view).

(a = anus, b = bladder, C.g. = Cowper's gland, ep. = epididymis, k = left kidney, pen. = penis, p.g. = prostate gland, r = rectum, sc. = scrotal sac (opened on left side), sp.c. = spermatic cord, t = left testis, u = left ureter, u.m. = uterus masculinus, v.d. = vas deferens.)

The male organs (Fig. 176), are a pair of testes, which originated on the dorsal wall of the abdomen, but descended, enveloped in the mesorchium, to the scrotum, as the animal reached maturity. The testis is an oval white body, closely applied to which is a yellowish mass of coiled tubes, the *epididymis*, which leads to the vas deferens. The spermatozoa formed in the testis pass through the epididymis. As the epididymis is strictly a part (mesonephros)

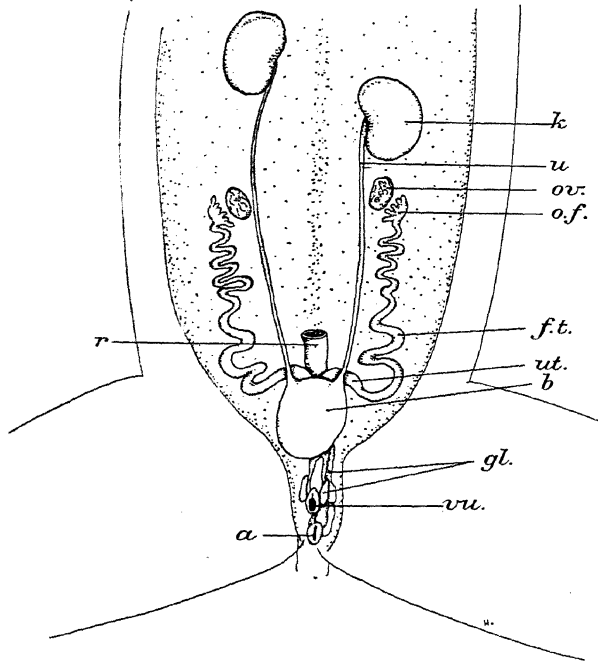


FIG. 177.—Urino-genital System of the female Rabbit (ventral view).

(a = anus, b = bladder, overlying the vagina, f.t. = Fallopian tube, gl. = glands, k = left kidney, o.f. = opening of Fallopian tube, ov. = left ovary, r = rectum, u = ureter, ut. = uterus, vu. = vulva.)

of the kidney, which descends with the testis to the scrotum, the spermatozoa of the rabbit enter kidney ducts for ejection, like those of the frog. The vasa deferentia pass up and over the ureters and enter a small median sac, the *uterus masculinus*, which opens into the neck of the bladder together with which it forms the *urethra*. As previously mentioned, the urethra leads to the end of the penis, which is provided with a nervous vascular swelling, the glans.

Associated with the urethra, and opening into it, are certain glands, the functions of which have not so far been satisfactorily explained. Lying beside the commencement of the urethra is a large muscular *prostate gland*, and lower down is a pair of smaller *Cowper's glands*.

The female organs (Fig. 177) consist of a pair of oval ovaries on the dorsal side of the abdominal wall near the kidneys. The ovaries have small projections on their surfaces which are the developing *Graafian follicles*, each containing a single egg which is released at the time of ovulation. Close to each ovary is the funnel-like opening of the oviduct, or *Fallopian tube*, a narrow convoluted tube which expands, as it passes towards the middle line, into a thick-walled *uterus*. The two uteri run close together, and open into a median *vagina*, dorsal to the bladder. The vagina and the neck of the bladder (urethra) unite to form the *vestibule*, which communicates with the exterior by the vulva. As in the male, Cowper's glands open into the urethra, but no prostate gland is present.

Fertilisation is effected within the body of the female, the male inserting the penis into the vulva of the female for the ejaculation of spermatozoa.

Eggs are liberated, when ripe, by the rupture of the Graafian follicles, and are taken into the Fallopian tubes. The spermatozoa, which are minute ciliated cells, travel up the oviducts to the eggs at the upper ends where fertilisation takes place. The fertilised egg, or *zygote*, commences to develop but moves down the tube to the uterus, where it is retained for the completion of its development. The resultant embryo possesses an outer investment, bearing projections which penetrate the wall of the uterus, and so become bathed by the blood of the mother. This intimate association of embryonic and maternal tissues produces a structure called the *placenta*. It is by means of the placenta that the embryo, or *foetus*, is nourished by the blood of the mother, which supplies both food and oxygen.

About four weeks after fertilisation, birth takes place, and although the young are blind and helpless, they are provided with the normal organs for a free life. After some weeks of feeding from the mammary glands of the mother the young are strong enough to begin their active life.

As the young of all mammals (with the exception of one class, the Monotremata, whose members actually lay eggs) are born alive, mammals are described as *viviparous*, in contrast to egg-laying animals, which are *oviparous*.

The Nervous System.

In its essentials, the nervous system of the rabbit agrees with that of the frog, and consists of the central nervous system, and the autonomic nervous system, which includes the sympathetic system.

The central nervous system is composed of the brain and the spinal cord, from which are given off cranial and spinal nerves respectively.

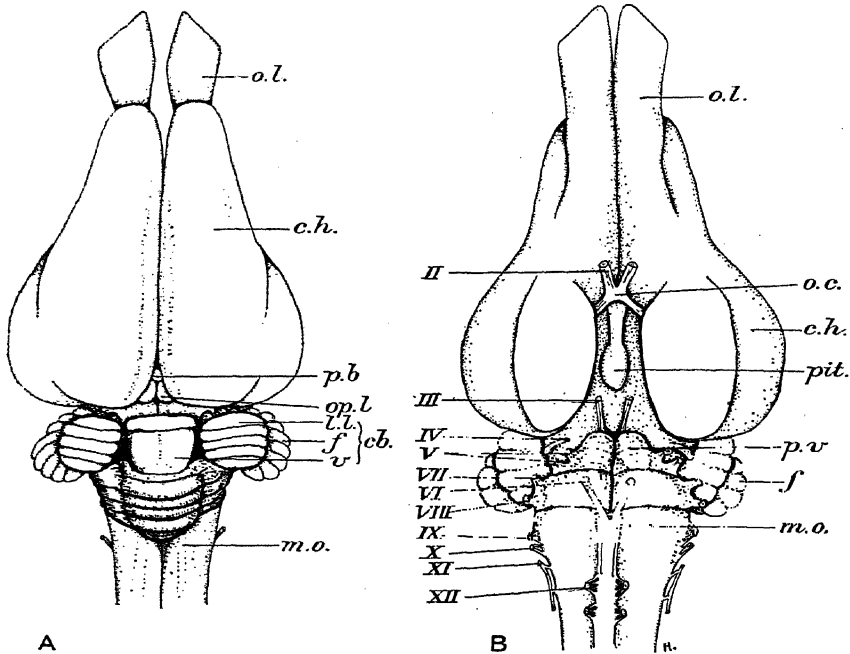


FIG. 178.—The brain of the Rabbit [$\times 2$].

A, dorsal view; B, ventral view.

(*cb.* = cerebellum, *c.h.* = cerebral hemisphere, *f* = flocculus (of cerebellum), *l.l.* = lateral lobe of cerebellum, *m.o.* = medulla oblongata, *o.c.* = optic chiasma, *o.l.* = olfactory lobe, *op.l.* = optic lobes (corpora quadrigemina), *p.b.* = pineal body, *pit.* = pituitary body, *p.v.* = pons Varolii, *v.* = vermis of cerebellum, *II-XII* = roots of cranial nerves.)

The brain (Figs. 178, 179) which occupies the cranium is protected by two vascular membranes, the *pia mater*, immediately covering it, and the *dura mater*, which forms the tough fibrous lining of the skull. Between these membranes is another, the *arachnoid*, which is separated from them in places to form spaces occupied by cerebro-spinal fluid.

The brain may be subdivided into fore-, mid- and hind-portions,

corresponding to the same regions in the frog but differing in the relative proportions.

The cerebrum consists of two large cerebral hemispheres, separated by a median fissure. In the rabbit the surface is almost smooth, but slight indentations occur, which foreshadow the great infolding of the surface of this part of the brain in the higher mammals, including man and the apes. The hemispheres are hollow, enclosing the lateral ventricles, and are not completely separated, as the inner adjacent walls of the ventricles are traversed dorsally by a band of fibres, the *corpus callosum*, a distinctive feature of the mammalian brain. On the lower side of each hemisphere an *olfactory lobe* runs forward to the nose, and projects beyond the anterior end of the hemisphere as a slightly swollen *olfactory bulb*. The back of the cerebrum overlies the thalamencephalon,

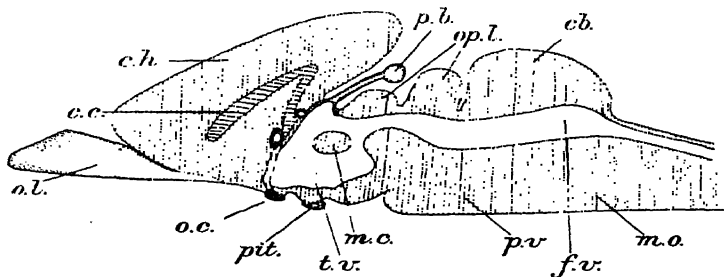


FIG. 179.—Diagrammatic median longitudinal section through the brain of the Rabbit.

(cb. = cerebellum, c.c. = corpus callosum, c.h. = cerebral hemisphere, f.v. = fourth ventricle, m.c. = middle commissure, m.o. = medulla oblongata, o.c. = optic chiasma, o.l. = olfactory lobe, op.l. = corpora quadrigemina, p.b. = pineal body, pit. = pituitary body, p.v. = pons Varolii, t.v. = third ventricle.)

the sides of which are thickened to form the *optic thalami*, whilst from the hinder end of its thin roof a pineal stalk passes upwards. The floor of the thalamencephalon carries the optic chiasma, behind which is the infundibulum with the pituitary body attached to it. The hollow cavity of the thalamencephalon is the third ventricle, connected to the lateral ventricles by the *foramina of Munro*, and traversed by a band of fibres, the *middle commissure*, connecting the optic lobes.

The dorsal part of the mid-brain bears the optic lobes, divided transversely to form two pairs of *corpora quadrigemina*.

In the hind-brain, the cerebellum is very prominent, being much more developed than that structure in the frog. It consists of a median lobe, the *vermis*, and a pair of convoluted *lateral lobes* which are united on the ventral side by a flat transverse band, the *pons Varolii*.

The hindermost part of the brain, the medulla oblongata, is broad in front but narrows posteriorly to become the spinal cord. Between the medulla and the cerebellum is the fourth ventricle, which has the thick medullary wall below, but is covered above by connective tissue, through an opening, the *foramen of Magendie*, in which, the cavity of the brain communicates with the arachnoid space.

The functions of the different parts of the brain have been ascertained from experiments with animals and the study of animal behaviour in disease and injury of the brain. The cerebrum contains centres connected with conscious sensations, voluntary muscle movements, intelligence and memory. The optic and olfactory lobes are concerned with sight and smell respectively, although, in man, certain visual centres are situated in the cerebrum. The cerebellum contains a number of centres concerned with body-balance, and the co-ordination of movement, such as of the limbs. The medulla is the seat of centres concerned with involuntary movements, including the heart-beat, and certain respiratory movements.

There are twelve pairs of cranial nerves, the first ten of which agree in name and main distribution with those of the frog. The eleventh nerve, the *spinal accessory*, supplies certain neck muscles, and the twelfth, the *hypoglossal* (a spinal nerve in the frog), supplies the tongue.

In dissecting the rabbit for the exposure of the nervous system, the neck region (Fig. 180) is of particular importance, for here may be seen several cranial and spinal nerves, and ganglia associated with the sympathetic system.

The tenth cranial nerve, the vagus, has an extended distribution. On emerging from the skull it swells into a *vagal ganglion* from which the *anterior (superior) laryngeal* nerve passes to the larynx. The right vagus passes ventral to the innominate artery, and the left vagus ventral to the aorta, after which, they send *posterior laryngeal nerves* to the larynx. The posterior laryngeal nerves ascend on either side the trachea and supply most of the laryngeal muscles. The main branches of the vagi then continue backwards, giving off branches to the heart, lungs, œsophagus, stomach and small intestine. Arising in the aortic region of the heart are two thin *depressor nerves*, which in the rabbit run upwards, parallel with the vagi, as far as the vagal ganglia, which they enter. They consist of fibres which convey impulses to the medulla, and result in certain reflex actions in the vascular system. In many mammals the depressor fibres actually run in the vagal nerve trunk.

The spinal cord is like that of the frog, and the spinal nerves arise in it by dorsal (sensory) and ventral (motor) roots, which form a mixed nerve which emerges between the vertebræ. The first spinal nerve passes from the cord between the skull and the atlas vertebra,

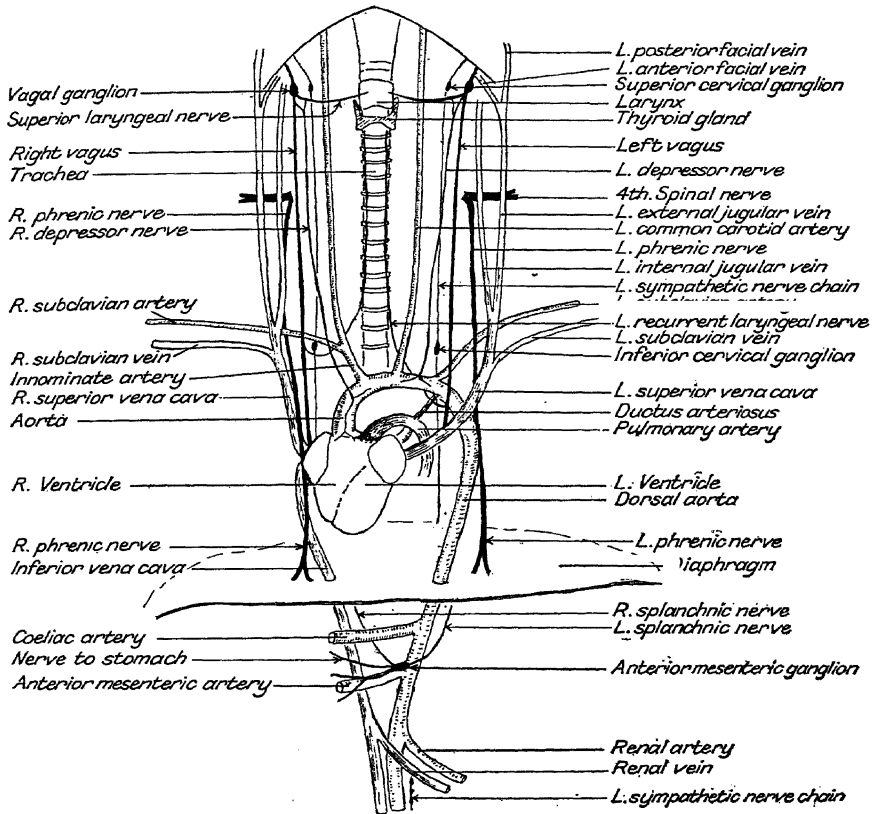


FIG. 180.—Diagram of the dissection of the neck and thorax of the Rabbit (most of the viscera have been removed; the anterior mesenteric ganglion is associated with the coeliac ganglion, which is not shown).

and the succeeding nerves emerge in front of the successive vertebræ along the trunk. The fourth and fifth spinal nerves give off branches which unite to form the *phrenic nerves* supplying the diaphragm (Fig. 180), passing under the anterior vena cava and over the subclavian artery of each side.

The organs of special sense associated with the central nervous system are in most respects similar to those of the frog. The ear of the rabbit (Fig. 181), is, however, more complicated than that of the frog, owing to the development, from the labyrinth, of a coiled *cochlea*, which is the true organ of hearing. The semi-circular canals present are, as in the frog, concerned with body balance. The external ear, or pinna, serves to concentrate the sound waves on to the tympanic membrane. The waves are transmitted by the auditory ossicles, across the middle ear to the fenestra ovalis, and thence by the endolymph to special cells in the cochlea. From these sensory cells of the cochlea nerve fibres run out and unite to form the auditory nerve, which transmits the impulses to the brain, which resolves them into sound.

The Endocrine Organs.

The rabbit possesses various *endocrine*, or *ductless, glands*, concerned with the liberation into the blood-stream of substances called *hormones*, which stimulate activity in some particular part or parts of the body. More is known of the endocrine secretions of mammals than of those of other animals, owing to the amount of experimental work which has been carried out on this group.

It has been found possible to indicate the functions of the endocrine glands, and even the various parts of the more complex ones, by noting the effects on growing animals, both of the removal of glands, and the administration of extracts containing the active hormones.

The *thyroid gland* is a bilobed organ lying across the larynx. It secretes *thyroxine*, which has an important effect on growth, for in its absence young animals remain of small size (Fig. 182, Plate VIII) and do not come to sexual maturity.

The *parathyroid* glands of the rabbit are minute bodies, often four in number, situated close to the thyroid. In many mammals, including man, the parathyroids are more or less embedded in the thyroid, so that removal of one often involves the removal of the other. The parathyroids secrete a hormone concerned with the maintenance of blood calcium at its normal level, but it is possible that other functions may also have to be assigned to it.

The *adrenal*, or *supra-renal, glands* of the rabbit are more clearly defined than those of the frog, being a pair of small yellow bodies anterior to the kidneys. The gland is composed of cortex and medulla, the latter secreting *adrenaline*, which, amongst other things, causes a constriction of arterioles (which produces a rise in blood pressure in the circulatory system), and a more vigorous heart-beat. Adrenaline is secreted particularly under conditions of emotion, asphyxia (suffocation) and exposure to cold. Its effects

are not prolonged, for, in common with other hormones, it is quickly destroyed by oxidation in the tissue fluids.

The *pituitary body* is a complex structure composed of *anterior* and *posterior lobes*, which are each concerned with the production of their special secretion. Its effects are extremely complicated and not yet fully understood, for it appears to have some influence over the other endocrine organs. The anterior lobe secretion is concerned, in some way, with the growth of the animal, for in its absence the skeleton does not develop satisfactorily, whilst if the secretion is abnormal, conditions of gigantism, or of a disease called acromegaly result. The posterior lobe secretion appears to contain several hormones, and two of its important effects are to cause the contraction of smooth muscle, and to raise the blood pressure.

Certain cells of the sexual organs are now known to have an endocrine function, the secretions of the testes and ovary influencing the acquisition of the distinctive characters of the male and female respectively.

The pancreas must be included with the endocrine organs, for although it is mainly concerned with the production of pancreatic juice, discharged by a duct into the duodenum, certain parts of it form a substance which is secreted directly into the blood. These parts are the *islets of Langerhans*, distinguished by the fact that their cells are not arranged in glandular form around a lumen, in contrast to the rest of the pancreas. The islets secrete *insulin* which plays a part in the carbohydrate metabolism of the body, stimulating the liver to build up glycogen from glucose. In the absence of insulin the body cannot use sugar, which is excreted in the urine.

The *thymus gland* has sometimes been considered to be an endocrine organ, but the general mass of evidence now discredits this view. In a young rabbit the thymus is a large pink organ lying in front of the heart over the origin of the arteries. As the animal matures, the gland progressively degenerates and a mere trace of it remains in the adult. As the gland is rich in lymphoid tissue, it may be associated with the formation of phagocytic lymphocytes during the juvenile life of the animal, when most protection against invading bacteria is necessary.

CHAPTER XXVI

SPECIAL ASPECTS OF ANIMAL NUTRITION.

VITAMINS

Previous chapters have dealt with the general structure and functions of the organs of the animal body. The general facts of animal nutrition have been stated, but there are several other aspects which need further consideration.

It has been indicated that animals require food material, in the form of carbohydrates, fats and proteins, which they obtain from plant or animal sources. This food is essentially similar to that of plants, and like it, supplies the organism with material for growth, and the energy for vital functions and movement. As in the plant, the more complex foods consumed by animals must be simplified before they become available to the living tissues. This is effected by enzymes, which are similar in nature and mode of action to those of the plant, save that in those animals with a digestive tract, the enzymes are *extracellular*, being secreted by the cells, in which they were formed, into the lumen of the alimentary canal, where they operate.

Animals have no power to elaborate organic food from simple inorganic raw material, and in starvation, when no ingestion of food is taking place, they waste and die, because of the lack of tissue repair, and energy for the maintenance of vital functions.

Although organic food is essential in animal nutrition, the higher animals, at least, cannot exist on a diet of *pure* carbohydrates, fats and proteins, but must be supplied with certain chemical elements in addition to those of the foods.

The important chemical elements include sodium, chlorine, calcium, potassium, phosphorus and iodine, and future experimentation may show the necessity of minute quantities of others.

Sodium occurs as sodium chloride and bicarbonate in the blood plasma and other tissue fluids. As chloride, it serves to produce an osmotic pressure essential for cellular activity, and together with potassium and sodium bicarbonate, it plays a part in the transport of the carbon dioxide of respiration.

Potassium, in addition to being concerned in the carriage of

carbon dioxide by the blood, is essential for the regulation of the heart-beat, and for muscular contraction.

Calcium is required for the formation of bones and teeth, and is concerned in the clotting of blood when shed. Blood plasma contains a number of proteins including *fibrinogen*, and it also contains a substance *prothrombin*. When blood is shed from a severed vessel, the blood-platelets disintegrate and liberate *thrombokinase* which activates prothrombin to form *thrombin*. Thrombin acts on the soluble fibrinogen and converts it to an insoluble network of fibrin, which forms a clot, serving to block the wound, so preventing further loss of blood. This series of reactions requires the presence of soluble calcium, for if blood is treated with potassium oxalate which reacts with dissolved calcium to form insoluble calcium oxalate, clotting will not occur.

Phosphorus is concerned in the formation of bones and teeth, the hard mineral part of which consists mainly of calcium phosphate and carbonate. Phosphorus occurs in the plasma as phosphate, which is partly involved in the maintenance of the reaction of the blood at such a value that the body will function normally. Phosphorus occurs in muscle as an organic compound, phosphagen, which is connected with the efficient contraction of the muscle fibres.

Iron is necessary for the formation of hæmoglobin in red blood cells, and the mammalian body requires a minute quantity of copper in order to utilise iron.

Iodine occurs in thyroxine of the thyroid gland. Its absence from human diet causes a deficient secretion of thyroxine, which causes the gland to enlarge in an attempt to form more secretory tissue, and produces a condition called *goitre*.

In addition to a suitable supply of organic food, water and inorganic salts, the animal body requires minute amounts of substances known as *vitamins*, or accessory food factors. The necessity of vitamins, in the nutrition of mammals and birds, has been proved in comparatively recent times, although the general action of substances, now known to contain them, in the amelioration of nutritional diseases, has been realised from ancient times.

When a young animal, such as an albino rat, is fed on a diet of pure carbohydrate, fat, protein, mineral salts and water, it ceases to grow, shows symptoms of disease and will eventually die. If, however, the animal receives, in addition, small amounts of material containing the essential vitamins, it grows normally and remains healthy. In the days of long sea voyages, when the food carried by ships was preserved, and the crews had no fresh rations, a disease called scurvy was prevalent. The great voyager, Captain

Cook, in 1776, described the cure of scurvy by the inclusion of fresh vegetables in the diet, and, about the same time, other people recorded its cure by the administration of lemon juice. In the nineteenth century, beri-beri, a disease causing a type of limb paralysis, was of common occurrence in eastern countries where the diet includes a large proportion of polished rice. Polished rice is supposed to be the best grade, for in its preparation the husk, aleurone layer and the embryo of the grain are removed. The crude grain, known as 'paddy' rice, includes the whole of the kernel.

An outbreak of beri-beri, of considerable interest, occurred amongst the prisoners in state prisons of the Philippine Islands, as a consequence of a humane government substituting the better-grade polished rice for the 'paddy' rice, which had previously formed a large part of the diet. As a result of this outbreak, the medical officer of a Javanese prison fed fowls on polished rice, and found that they soon developed the disease of polyneuritis, which is the equivalent of beri-beri in birds. When a small amount of rice embryo was added to the polished rice diet, the disease disappeared, indicating that polyneuritis was due to an absence from the diet of some accessory factor, carried, in this case, in the rice embryo.

In this country, Professor Gowland Hopkins, investigating the dietetics of milk, established the necessity of accessory food factors. He selected two groups of young rats, and fed one on a diet of pure starch, casein (a protein of milk), lard and essential salts, whilst the other group received a similar diet, together with a small daily quantity of fresh milk. It was found that the second group steadily increased in weight whereas the first group gradually lost weight. At the end of three weeks the diets of the two groups were reversed, which resulted in the first group (now receiving fresh milk), increasing in weight, and the second group, deprived of milk, lost weight. From the point of view of energy supply, the two diets were identical, so the failure of growth was evidently due to the absence of an accessory growth-promoting substance, supplied by fresh milk in the case of the growing rats.

By numerous experiments of a similar nature, and by investigating the effects of diet on man, the necessity of vitamins is now fully established, although, as yet, their chemical nature and mode of action in the body are not completely elucidated.

A vitamin may be described as an organic substance which is not a food, but is essential to the nutrition of any animal which cannot synthesise it.

At present there are six established vitamins, each denoted by

a letter, but it seems probable that the number will be added to in the future.

It appears that vitamins are synthesised by green plants, from which herbivorous animals obtain them, thus making them available to carnivorous animals, which obtain them from the flesh of other animals. It may be, however, that the plant supplies the animal with a precursor, which is converted into the vitamin within the animal body, as is evidenced by the relation of carotin to vitamin D.

The vitamins A and D, which occur in cod-liver oil, are also present in the oil contained in the cells of a microscopic marine Alga, which has built them up from inorganic sources. The Alga is eaten by small marine animals, which serve as food for small fish, which in their turn provide the food of the cod. In the chain of nutrition involved in this example, presumably the vitamins are passed on, so that they appear later in the liver oil of the cod, one of the important commercial sources of vitamins A and D.

The vitamin of butter is closely related to the pigment carotin, contained in the green plant food eaten by the cow, so that a butter richer in vitamin is obtained from the milk of cattle fed on green-stuff, than from cattle fed on oil-cake and similar food.

The known vitamins have been classed as *fat-soluble*, and *water-soluble*, the former being vitamins A, D and E, and the latter B₁, B₂, and C.

Vitamin A has been called the growth-promoting vitamin, as, in its absence from the diet of young animals, growth ceases, and they may die. As the vitamin protects the body from certain bacterial infections, it is best considered as the anti-infective vitamin, and in its absence, an eye-disease, xerophthalmia, and pyorrhoea, a disease of the gums, may occur. Vitamin A is present in liver oils, those of the cod and halibut being rich sources, butter, milk, beef-fat, egg-yolk and fresh green vegetables. It is absent from vegetable oils, yeast and cereal grains.

In herbivorous and omnivorous animals, the vitamin is built up from carotin derived from plants. Pigs fed on red palm oil, a substance containing abundant carotin, but no vitamin A, were found to have liver oil very rich in this vitamin, which indicated its synthesis within the animal.

Vitamin D is known as the anti-rachitic vitamin, for in its absence a disease, rickets, occurs. Rickets is due to a disturbance of mineral deposition in bones, causing them to be weak, so that they bend when the strain of the body-weight is placed on them. Rickets can be cured either by the administration of vitamin D, or by exposure of the body surface to sunlight, facts which led to

the discovery of the chemical nature of the vitamin, the first to be prepared in a comparatively pure state. Animal skin contains cholesterol, a substance related to the fats, which contains a small amount of another substance, ergosterol. When ergosterol is exposed to sunlight, vitamin D is formed, and this occurs when the skin is irradiated, even when no vitamin is included in the diet.

Vitamin D is often associated with vitamin A, as in cod-liver oil, animal fats and liver oils, and egg-yolk. The vitamin is not present in cereals, and is present in very small amounts in green vegetables.

Vitamin E is necessary for reproduction in certain mammals, and when absent, the male reproductive cells fail to develop, and the female is incapable of producing offspring. It occurs in green vegetables, wheat-embryo oil and some other vegetable oils, but is absent from most animal oils.

Vitamin B consists of at least two fractions, at present known as B₁ and B₂. Vitamin B₁ is the anti-beri-beri vitamin, and B₂ is the anti-pellagra vitamin, pellagra being a disease causing pronounced digestive disturbances, and skin eruptions in those parts of the body exposed to light. Remarkable recoveries result from the administration of small amounts of the vitamin to subjects suffering from deficiency diseases.

Rich sources of vitamin B are the bran and embryo of cereal seeds, which contain both B₁ and B₂, with the exception of maize which contains B₁ only. Yeast and yeast extracts contain both parts of the vitamin, and in the hen's egg B₁ is present in the yolk and B₂ in the 'white.' Vitamin B₁ is destroyed by steam heat of over 100° C., but B₂ resists destruction under such conditions.

Vitamin C, the anti-scorbutic vitamin, is concerned with the prevention of scurvy. It is present in citrous fruits, like lemons and grape-fruit, in tomato fruits and green vegetables. It is practically absent from dry seeds, but is formed by the seedlings on germination. This fact was used in the treatment of an outbreak of scurvy in Serbia in 1918 when infusions of germinated seeds were administered to scurvy patients.

Vitamin C has been isolated, and its chemical nature determined. It has been prepared synthetically under the name of ascorbic acid.

Vitamin shortage in human diets is now of rare occurrence, except in regions where fresh food is not easily obtained, such as was the case in certain countries during the European War. Unfortunately modern diets include a large proportion of cooked and canned foods which may not contain the vitamins present originally in the fresh material.

Vitamin A is destroyed by heat, as is vitamin C, which is very

unstable and is destroyed by sun-drying. Fruits and milk contain vitamin C, but stewed fruit and pasteurised or boiled milk do not.

Vitamin B is more stable than A and C, but the water-cooking of vegetables usually results in some loss of the vitamin. It is sometimes a practice to add soda to the water in which green vegetables are boiled in order to preserve the green colour, but owing to the alkaline conditions produced, vitamins B₁ and C are destroyed. Vitamin D is not easily destroyed by heat, and, as it can be formed in the skin by exposure to sunlight, there is rarely any shortage of it.

CHAPTER XXVII

PARASITIC ANIMALS. THE MALARIAL PARASITE. THE LIVER FLUKE

During the evolution of animals, a number of forms have adopted a parasitic mode of existence, attaching themselves intimately to the bodies of other animals, which supply them with food.

There is little doubt that such parasites were derived from normal ancestors, as, in most cases, they retain sufficient characters to be assigned to the various animal groups, which are mainly composed of types with the usual methods of nutrition. Animal parasites are of wide occurrence and may be of considerable importance when their host happens to be either man or a domestic animal. Human diseases, due to animal parasites, include malaria, sleeping sickness, and amœbic dysentery, all caused by specific Protozoa, whilst the presence of tapeworms in the intestine may result in under-nourishment and wasting of the body.

Few vertebrate animals are parasitic, but those which are, include the lamprey and the hag-fish, which attach themselves to the surface of other vertebrate hosts from which they obtain food. The vertebrates, because of their highly organised bodies, with accessible organs affording satisfactory protection to the parasites, are extensively parasitised by a great variety of organisms.

Animal groups, which include numerous parasites, are the Protozoa, Arthropoda, Round-worms and Flat-worms.

The vast majority of parasitic animals are *endoparasites*, such as the malarial parasite and the liver-fluke, living within the body of the host, in contrast to the lice and ticks, which are *ectoparasites* attached to the surface of the host from which they suck food.

Most parasitic animals possess the habit throughout life, but some, such as the ichneumon flies, are parasitic in their larval stage only.

Several animals are *facultative parasites*, living free under some conditions, but entering the body of a host under others. Such a form is a roundworm, *Leptadiera*, which lives in damp soil, but can parasitise a slug, *Arion*, in which event it loses its mouth, and applies more of its food to the production of eggs.

Some parasites complete their development in one host, but

others require two hosts in order to complete their life-cycle. In the latter case, the host in which the parasite carries out sexual reproduction is called the *primary host*, and the host in which it completes its development, frequently involving asexual reproduction, is the *secondary*, or *intermediate host*. As will be seen later, this type of parasite is more easy to control, for, if one or other of the hosts is removed, the multiplication of the parasite will be prevented and the animal eradicated.

In some cases a parasite has become specialised for life within a particular host, the tapeworm, *Tænia solium*, which lives in the intestine of man, appears to be incapable of developing (in the same stage) elsewhere. On the other hand, a number of Protozoan parasites called Trypanosomes, develop equally well in a variety of hosts.

The parasitic method of life results in structural and physiological changes in the animal. Owing to the comparative ease with which a parasite obtains food, there is little need for it to retain the power of locomotion. In the case of certain Crustaceans, the Rhizocephala, which parasitise other Crustaceans, the crabs, the animals have lost their limbs, which are such a characteristic of the phylum Arthropoda, of which they are members. In the liver fluke, to be dealt with in detail later, the animal is non-motile or sluggish when occupying the alimentary tract of its primary host, the sheep. It forms a free-swimming larva in order to reach its secondary host, a water-snail, and later on forms another motile structure to reach a suitable position for entry into the body of another sheep. With a loss of motility, it is not unusual for the larger endoparasites to develop some structure for intimate attachment to the tissues of the host. The tapeworms attach themselves to the intestinal wall of the host by suckers and hooks, otherwise they would be ejected from the body.

Associated with the easy access to food material, the alimentary system of parasitic animals undergoes simplification. Some forms merely lose their masticating organs, but others, like the tapeworms, which are continually bathed in fluid food, have no alimentary system at all.

The respiratory systems of endoparasites have disappeared from those forms which must be derived from ancestors presumed to have possessed them. The respiration of endoparasites is not fully understood, for, whilst it can be realised that such types as the malarial parasites, which live in the blood, have little difficulty in obtaining oxygen, it is not easy to suggest whence the oxygen is derived for such animals as the tapeworm and other intestinal parasites. It may be that parasites so situated as to have difficulty

of access to oxygen can carry out anærobic respiration, utilising the sugars and glycogen, provided by the host, for the process.

With the adoption of the endoparasitic habit the nervous system is liable to disuse. In the ordinary free-living animal, the primary functions of the nervous system are to acquaint the animal with the happenings in its vicinity, but an endoparasite is largely protected from circumstances necessitating a response, and the nervous system is either poorly developed or completely absent.

Even though the parasite may have no nervous system, or one of feeble development, it can be capable of response to stimuli, otherwise animals like the liver fluke, which reaches the bile duct of the sheep, after having entered the intestine with food, and *Monocystis*, which develops in the seminal vesicles of the earth-worm after entering its digestive tract with food, could not take up their usual positions in the body of the host. The migration of parasites to particular organs and tissues is probably a case of chemotaxis, the organism responding to some characteristic substance formed, or possessed by, the tissue.

An important feature of parasitic animals is their great power of reproduction. Even when most other systems of the body have undergone degeneration, the reproductive system remains well-developed. In a parasitic Arthropod, *Sacculina*, which is attached to the abdomen of the crab, the body is a sac containing little more than the sexual organs.

Frequently the parasite is hermaphrodite, so that, as the male and female organs are in close proximity, a high percentage of fertile eggs may result.

Specific methods of transmission of a parasite from host to host will be dealt with in considering the animal parasites below. Human diseases due to parasites may be carried to new hosts in food and water, as well as by blood-sucking insects. Bacterial diseases are due to minute plant parasites, and include tuberculosis, cholera, and anthrax. Such diseases may be transferred by blood-sucking insects such as fleas, which are known to carry bubonic plague bacteria from rats to man. They can also be carried in water, and in the air, and occasionally (as in anthrax), the parasite gains entry through a wound in the skin with which it has come in contact.

The Malarial Parasite (Fig. 183)

Malaria is a human disease prevalent in certain tropical regions, but occasionally met with in more temperate climates. It was at one time common in the Fen district, the Thames Valley, and other low-lying parts of Britain, being known as ague, which was thought to be due to the inhalation of foul air arising from the swampy soil.

In 1882 a French doctor, Laveran, discovered the presence of Protozoan parasites in the blood of malarial patients, and late in

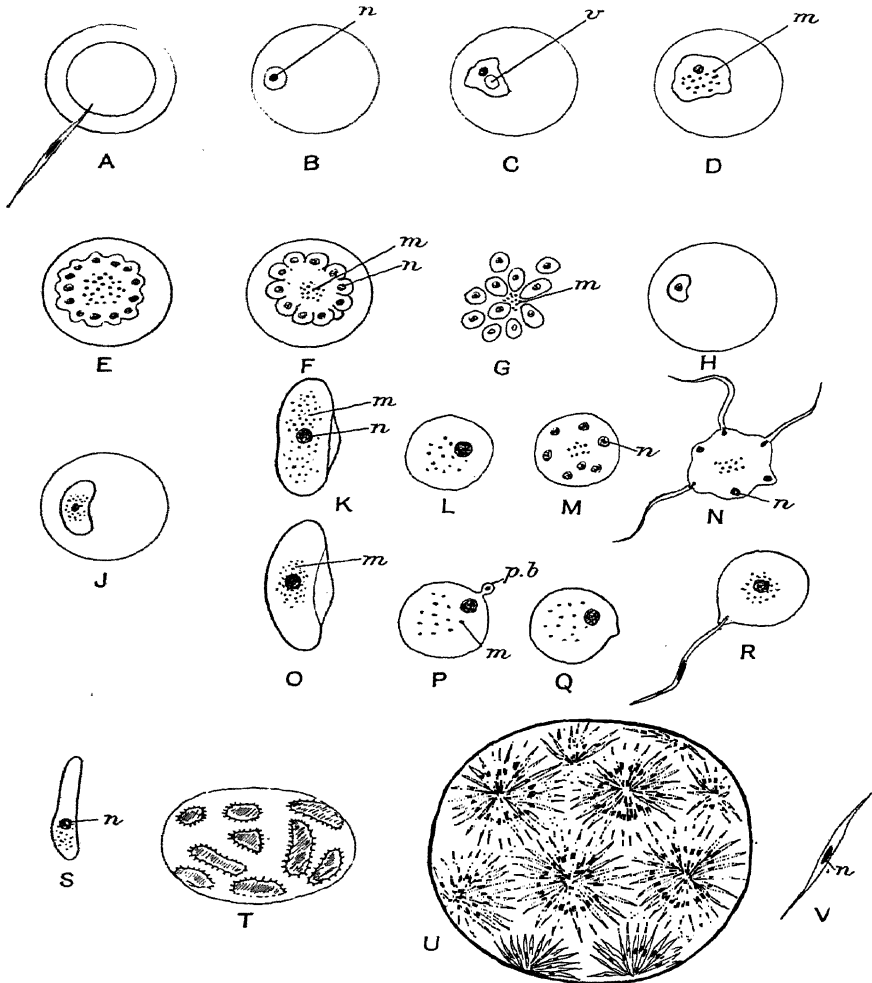


FIG. 183.—The life-history of a Malarian parasite (*Plasmodium immaculatum*).

A, sporozoite entering human red blood cell; B–G, development of merozoites; H, J, development of gametocyte; K, male gametocyte in red blood cell; L–N, formation of microgametes in stomach of mosquito; O, female gametocyte in red blood cell; P–R, formation of megagamete in stomach of mosquito; S, zygote; T, oocyst containing sporoblasts; U, mature oocyst, with numerous sporozoites, in stomach-wall of mosquito; V, single sporozoite.

(*m* = melanin granules, *n* = nucleus, *p.b.* = polar body, *v* = vacuole.)

the nineteenth century Ross and Grassi, independently, demonstrated that the parasite was transmitted to human hosts by certain mosquitoes.

The prevalence of the disease in swampy regions is easily understood, when it is remembered that the mosquito requires water in order to breed. The transmitting mosquito is a member of the Anopheline group, and only the blood-sucking females carry the parasite. In the absence of such insects malaria cannot be transmitted to new human hosts, an important fact which enables the disease to be controlled with fair success.

Three types of malaria are common, each caused by a particular parasite belonging to the Protozoan class, Sporozoa.

Benign tertian malaria is caused by *Plasmodium vivax*, benign quartan malaria by *Plasmodium malarie*, and malignant or pernicious malaria by *Plasmodium immaculatum*.¹ Each type of the disease has its characteristic symptoms, including, amongst other things, the intervals between the attacks in an infected subject.

There is a general similarity in the life-cycle of the species of *Plasmodium*, and the description which follows applies to all.

The parasite completes its full life-cycle in two hosts, the mosquito being the primary host, and man the secondary host, and whereas the parasite causes considerable discomfort to the human host it appears to cause little disturbance in the mosquito.

In man, the parasite develops in the blood-stream, to which it gains entry from a female mosquito, which has penetrated the human skin in order to suck blood from the tissues. The formation of the wound in itself is unimportant, for if man is bitten by *Culex pipiens*, a common British mosquito, which does not carry the parasite, no malaria can result.

The salivary glands of the Anopheline mosquito contain microscopic needle-like uninucleate cells, the *sporozoites* of *Plasmodium*, which are injected into the wound when saliva is secreted by the female mosquito during its blood-sucking operations. From this point the parasite continues its development in the human blood.

Having entered the blood, the sporozoite penetrates the membrane of a red blood cell which it enters, assumes an amoeboid shape (Fig. 183, B), and enlarges at the expense of the cell substance. It is now called a *trophozoite*, as this is the main feeding stage in the life-cycle. As growth continues, a large vacuole is formed near the nucleus, and granules of a dark pigment, *melanin*, appear in the cytoplasm (Fig. 183, C, D). Ultimately when the trophozoite occupies practically the whole of the blood cell, the nucleus divides into about sixteen parts, followed by segmentation of the cytoplasm

¹ Also known as *Plasmodium falciparum* and *Laverania malarie*.

which discards the melanin (Fig. 183, E-G). This is the asexual method of reproduction, known as *schizogony*, in which a number of rounded uninucleate *merozoites* are formed. The merozoites escape into the plasma by the rupture of the membrane of the blood cell, and if not subsequently destroyed by leucocytes, invade new uninfected red cells and repeat the process.

It is the occurrence of schizogony which causes the onset of the attacks to which a malarial patient is subject, these coinciding with the liberation of the merozoites. The process occupies from one to three days according to the species of *Plasmodium*. Owing to the destruction of red cells the malarial patient suffers from anaemia, but various other symptoms occur in the liver, spleen and kidneys, through which the blood, containing by-products of the parasite's metabolism, flows.

After a time the sexual forms of the parasite, known as *gametocytes*, are formed from some of the later merozoites, which enter the red cells (Fig. 183, H, J).

Plasmodium is unisexual, and forms male, or *microgametocytes*, and female or *megagametocytes*. The gametocytes of *Plasmodium vivax* and *malariae* are round or elliptical, and about the size of the mature trophozoite, whilst those of *Plasmodium immaculatum* are crescentic, and stretch across the red cell which contains them (Fig. 183, K, O). The male and female gametocytes may be distinguished in some cases by the position of the melanin granules which are close to the nucleus of the female (Fig. 183, O), but more dispersed in the male (Fig. 183, K). The gametocyte can undergo no further development until it is taken up into the body of the particular mosquito. If, for instance, blood containing gametocytes was sucked into the stomach of a Culicine mosquito, the parasite would be digested along with the red cells, and the life-cycle would be terminated.

Within the stomach of the Anopheline mosquito the gametocytes are set free from the red cells on the digestion of the latter, and are stimulated to continue their development.

The megagametocyte assumes a rounded form, its nucleus divides unequally into two and the smaller part is extruded with a small amount of cytoplasm, as a *polar body* (Fig. 183, P). The remaining nucleus and cytoplasm form the relatively large female- or *mega-gamete*.

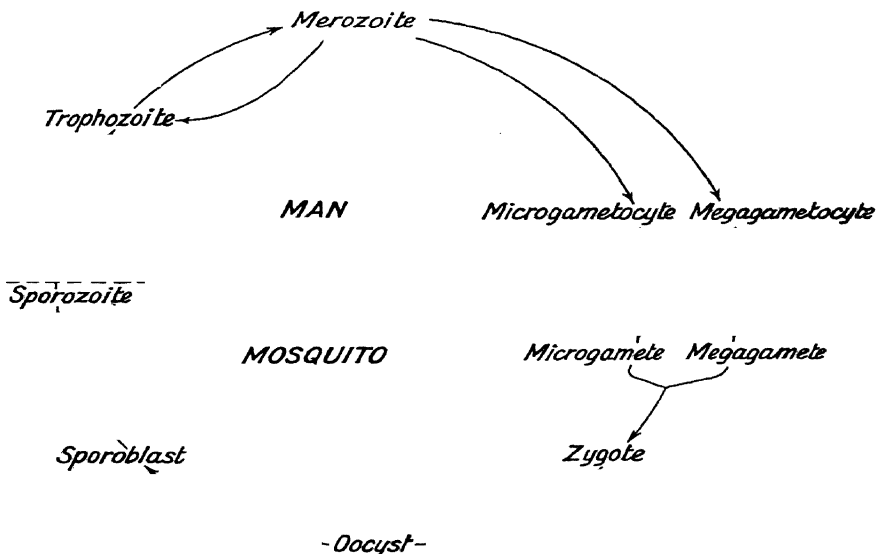
The microgametocyte becomes rounded, and by pseudopodial developments forms a number (four to eight) of slender processes at its periphery (Fig. 183, N). The nucleus divides into several parts, and as the main body of the microgametocyte contracts, one nucleus enters each of the processes which are set free as the male-, or *micro-gametes*, capable of sinuous movement.

Prior to fertilisation the female gamete forms a small outgrowth, the *perception cone*, at one side, and when a microgamete touches this it adheres, and subsequently enters the female cell (Fig. 183, R), fertilisation being completed with the fusion of the male and female nuclei.

The zygote formed elongates (Fig. 183, S), and passes through the epithelial lining of the mosquito's stomach into the sub-epidermal tissue in which it develops into a thin-walled *oocyst*. At this stage, as numerous zygotes have usually been formed in the stomach, the outer surface of the stomach bears several projecting nodules, each containing an oocyst. By continued division of the oocyst nucleus and its cytoplasm, a number of round *sporoblasts* are formed (Fig. 183, T), and by continued nuclear division, within them, a mass of slender *sporozoites* is formed (Fig. 183, U). As a result of this, the oocyst becomes much enlarged and projects into the other tissues of the insect, finally bursting to liberate the sporozoites into the blood sinuses. Sporozoites may now be carried to the salivary glands, and by penetrating their secretory cells are available to infect a new human host, and so continue the life-cycle.

The sexual process is called *sporogony*, and occupies from eight to twelve days under ordinary circumstances, but is somewhat quicker in tropical climates than under temperate conditions.

The life-cycle of the malarial parasite may be summarised thus :



The Liver Fluke (*Fasciola hepatica*)

The liver fluke is an endoparasite occurring in the bile-duct, and the branches of the portal vein of the liver of sheep. Its presence causes a disease called liver-rot, which generally proves fatal, and is most prevalent in damp localities. This parasite may be found in other mammalian hosts, including the horse and ox, and on rare occasions it has been found in man, who may have been infected through eating watercress.

The liver fluke is a member of the class Trematoda, of the phylum Platyhelminthes, which includes a number of flat-worms such as the flukes, tapeworms and other parasites of similar nature.

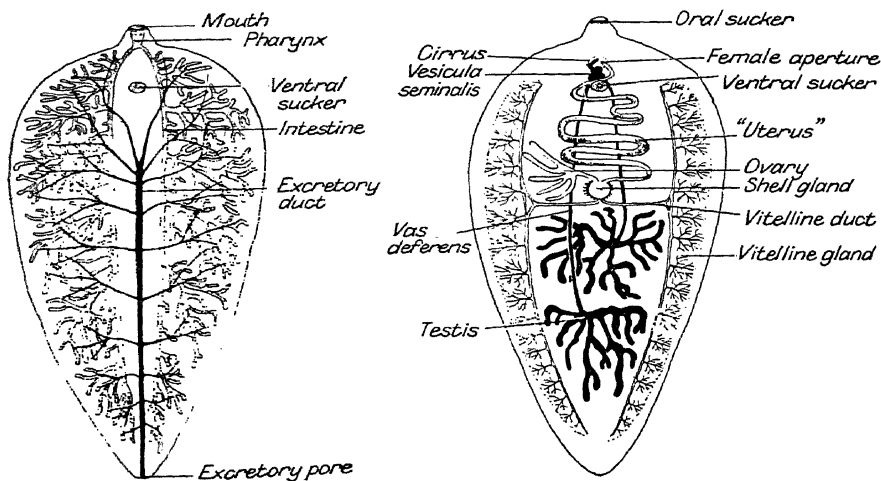


FIG. 184.—The Liver Fluke (*Fasciola hepatica*) [$\times 2\frac{1}{2}$].

A, digestive and excretory systems; B, reproductive system.

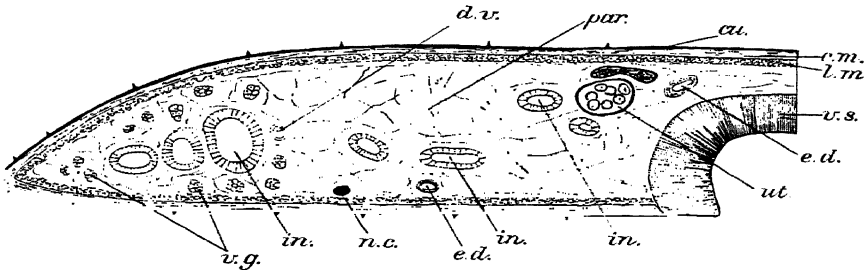
It requires two hosts for the completion of its life-cycle, the sheep, or another mammal, being the primary host, and a small water-snail, the intermediate host.

The adult animal (Fig. 184), found in the bile-duct of the sheep, is a flat, oval organism, about $\frac{3}{4}$ to 1 inch in length and about half as wide at its broadest part. The anterior end is slightly pointed, and terminated by a mouth surrounded by a circular sucker which serves to assist the animal's attachment to the wall of the bile-duct. There is a second larger **posterior sucker** on the ventral side of the body in the middle line, slightly anterior to the broadest part of the body.

The body is protected externally by a thick cuticle bearing small

backwardly-directed projections, or *spinules*. Beneath the cuticle are two layers of muscular tissue, the outer layer consisting of transverse fibres, the inner fibres being longitudinally arranged (Fig. 185). Within the body-wall are alimentary, excretory, reproductive and nervous systems, and the space not taken up by these is occupied by a parenchymatous connective tissue so that no coelom exists.

The alimentary system commences with the mouth which leads to a short muscular pharynx from which the intestine passes. In the region of the ventral sucker, the intestine bifurcates, and the branches pass laterally down either side of the body, near the margin, ending blindly near the posterior end. The intestine branches repeatedly to ramify amongst the other tissues which it supplies with food. The ingested food is almost wholly liquid, so that there



g. 185.—Half of a transverse section through the body of the Liver Fluke (*Fasciola*), in the region of the ventral sucker (diagrammatic).

(c.m. = circular muscle, cu. = cuticle (ectoderm), with spinules, d.v. = duct of vitelline gland, e.d. = duct of excretory system, in. = intestine, l.m. = longitudinal muscle, n.c. = nerve, par. = parenchyma, ut. = 'uterus,' with eggs, v.g. = vitelline gland, v.s. = ventral sucker.)

is no need for an aperture for the excretion of fæces. Soluble waste matter, produced during the metabolic activities of the body, is excreted by a special *protonephridial system*. Scattered through the parenchyma of the body are numerous hollow cells, within each of which is a tuft of cilia projecting into the cavity. These are the *solenocytes*, or '*flame-cells*,' so called because of the appearance presented by the flickering bunch of cilia which sets up a current from the cell. Waste matter is extracted from the other tissues by the 'flame-cells' and transferred to a central canal produced by a number of tubular cells, which form intracellular ducts leading to a central canal. The central canal passes to the posterior end of the body, where the waste is voided through an *excretory pore*.

The nervous system is poorly developed, and consists of a ring of nerve fibres surrounding the pharynx. The nerve-ring bears

a pair of lateral ganglia, from which fibres pass forward to the mouth and sucker, and backwards, as a pair of lateral nerves, to the hinder end of the body. There are no special sense organs.

The reproductive system (Fig. 184) is highly developed, and the animal is hermaphrodite. The male organs consist of two branched testes lying near the middle of the body. Each ends in a vas deferens which passes forward to the region of the ventral sucker where it unites with the other in a common sac, the vesicula seminalis. From the vesicula seminalis, the *ejaculatory duct* leads to the surface, opening on the ventral side of the body, anterior to the sucker. The end of the male duct takes the form of a short protrusible penis, or *cirrus*, apparently concerned with fertilisation.

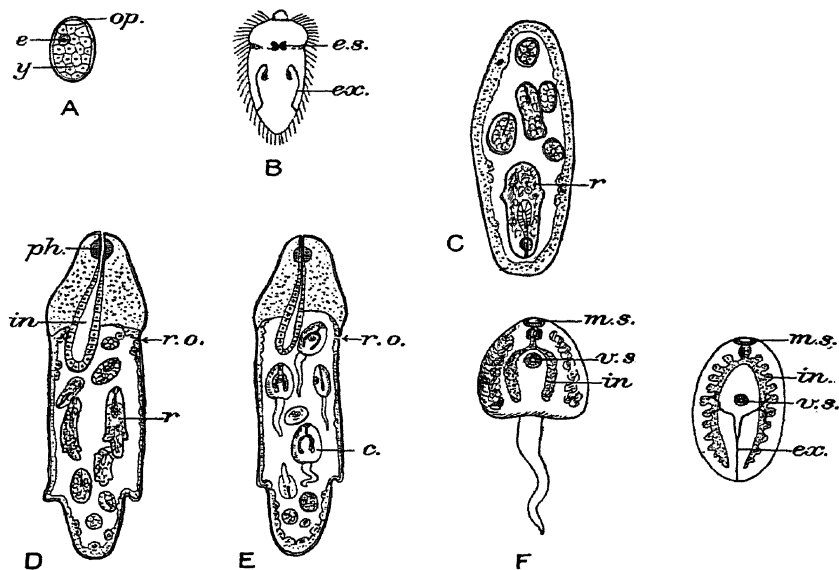
The female organ is a single-branched ovary in the middle of the body. From it an oviduct leads to the *shell-gland*, a mass of glandular cells concerned with the secretion of a shell around the fertilised egg. In its way to the shell-gland, the oviduct receives the *vitellarian duct* formed by the union of the ducts of two large *yolk-glands* which lie on each side of the body. At this point, also, a short duct, *Laurer's canal*, communicates with an opening on the dorsal side of the body. From the shell-gland, the oviduct passes forward as a wider convoluted tube, or 'uterus,' which ends at the surface, close to the male aperture.

The method of fertilisation of the eggs set free from the ovary is not known, but it seems probable that spermatozoa, from another animal, are introduced by the cirrus into Laurer's canal. After fertilisation, the eggs, which are produced in large numbers, receive a supply of yolk and each is enclosed in a chitinous shell secreted by the shell-gland. The eggs are then passed to the 'uterus,' and are finally discharged into the bile-duct of the host, from whence they pass into the intestine, and are passed out of the sheep with the faeces.

After lying on the herbage for some weeks, the egg-case is broken, by the splitting of a lid, or *operculum*, which liberates a microscopic larva. The larva, or *miracidium* (Fig. 186, B), has a ciliated surface, which enables it to progress through the moist grass towards ditches and ponds inhabited by the secondary host, a water-snail, *Limnaea*. The miracidium is a short-lived stage, and unless it reaches a suitable host within about 8 hours, it dies.

On reaching the snail, the larva bores into the respiratory chamber, or other organ of the host, and loses its cilia. It then grows into an elongated *sporocyst* (Fig. 186, C), about 5 millimetres in length, which contains a cavity from the lining of which cells are

budded off to develop into oval individuals, known as *redia* (Fig. 186, D). On liberation the redia may form daughter-redia by a similar budding into its internal cavity, or it may form other individuals called *cercariae* (Fig. 186, E). The cercaria (Fig. 186, F) is a small oval body with an elongated tail, which enables it to move about. It possesses anterior and ventral suckers, pharynx and bifurcated intestine. The cercaria forces its way out of the snail's body, swims about free in the water for a short



g. 186.—Stages in the life-cycle of the Liver Fluke (*Fasciola hepatica*), all much enlarged.

A, egg; B, miracidium; C, sporocyst with developing redia; D, redia, containing developing daughter-redia; E, redia, containing developing cercariae; F, cercaria; G, young liver-fluke.

(c = cercaria, e = egg-cell, e.s. = eye-spot, ex. = excretory system, in. = intestine, m.s. = oral sucker, op. = operculum, ph. = pharynx, r = daughter-redia, r.o. = reproductive opening, v.s. = ventral sucker, y = yolk-cells.)

time, passes to the edge of the ditch, and after losing its tail, attaches itself to grasses or other plants, and becomes encysted. Sheep grazing in the vicinity of water may eat herbage bearing the cysts. On arrival in the intestine of the sheep, the cyst liberates the young liver fluke (Fig. 186, G), which migrates to the bile-duct and commences to become a mature adult.

Infection of sheep generally occurs in the autumn, and the parasite remains in the host from nine to fifteen months. The

effect of the parasite on the sheep is to produce anaemia, accompanied by such other symptoms as wasting and loss of wool.

The control of liver-rot consists either in the transference of sheep to dry pastures, where the intermediate host is not likely to be present, or in draining wet pastures to make conditions unsuitable for the development of water-snails.

CHAPTER XXVIII

ANIMAL DEVELOPMENT. EMBRYOLOGY OF THE FROG AND THE CHICK

In the majority of animals the formation of new individuals is the result of sexual reproduction. The higher animals, such as the amphibians and the mammals, use no other method, whilst in animals like *Paramecium* and *Hydra*, which may use asexual reproduction, sexual means must be resorted to if the animal is to survive. Animals may be hermaphrodite, or bisexual, as the earthworm and the liver fluke, but they are, more commonly, unisexual, either male or female. In both cases the formation of the sexual cells follows the same general lines, and, except in the Protozoa, this takes place in the special reproductive organs, or *gonads*.

Male and female gametes are characteristically dissimilar, the male gamete, or spermatozoon, being a small motile cell, in contrast to the female gamete, which takes the form of a relatively large, passive egg-cell, or ovum. The fusion of male and female gametes in fertilisation institutes a new cell, the zygote, which undergoes a development characteristic of the animal to which it will give rise. As, in fertilisation, two distinct cells fuse, it is clear that the resulting zygote will contain twice the number of chromosomes found in the individual gametes. Therefore, in order to avoid the doubling of chromosomes with each subsequent fertilisation, it is essential that the gametes shall have but half the number of chromosomes found in the zygote. The ordinary *somatic cells* of an animal possess nuclei with a diploid chromosome number, as do the mother-cells of the gametes. When the gamete-mother-cell divides to form the gametes, or *germ-cells*, it undergoes a reduction division, essentially similar to that which occurs in the formation of the spores of the male fern (p. 159). By this means, the gametes come to possess haploid nuclei, and the normal diploid nucleus is reinstituted in the zygote.

The process by which gametes are formed is called *gametogenesis* (Fig. 187), which may be either *spermatogenesis*, when spermatozoa are formed, or *oogenesis*, when ova are formed.

As an example of these processes, the maturation of the germ

cells of the frog may be taken, as the general events are similar to those in other animals.

Spermatogenesis occurs in the testes, which are composed of seminiferous tubules, the epithelial lining of which consists of cells undergoing division. Certain diploid cells formed by the **germinal epithelium** are the sperm-mother-cells, or **spermatocytes**, which

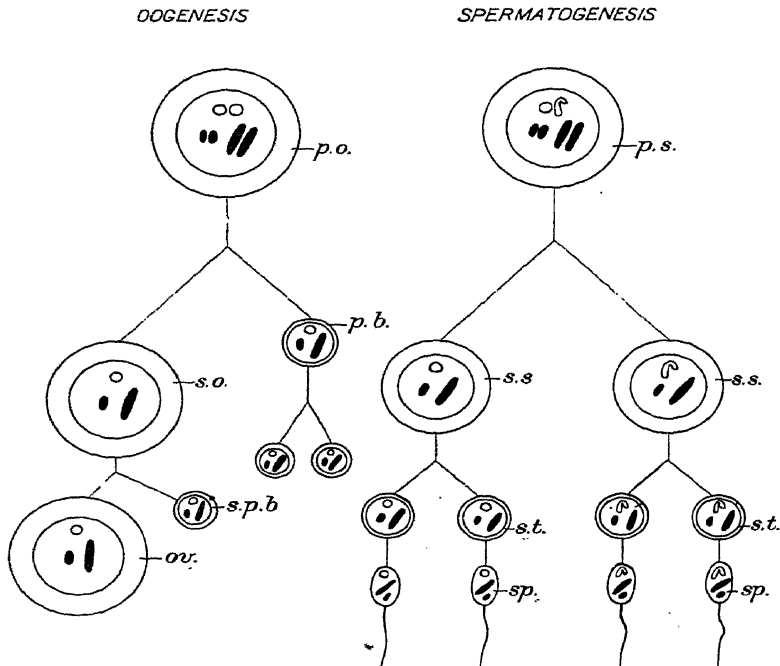


FIG. 187.—GAMETOGENESIS. Diagram to illustrate the maturation of the germ cells of an animal, in which the *diploid* chromosome number is 6, and the female carries the two *sex*-chromosomes (denoted by small circles, the Y-chromosome, of the male, being curved).

(*ov.* = mature ovum, *p.b.* = first polar-body, *p.o.* = primary oocyte, *p.s.* = primary spermatocyte, *s.o.* = secondary oocyte (haploid), *sp.* = spermatozoon, *s.p.b.* = second polar-body, *s.s.* = secondary spermatocyte (haploid), *s.t.* = spermatid.)

are projected into the lumen of the tubule by the enlargement of other **sustentacular** cells, which also serve to nourish the spermatocytes. The nucleus of each spermatocyte undergoes two successive divisions which constitute meiosis, and result in the formation of four equal haploid nuclei. This is followed by a division of the cytoplasm of the spermatocyte to form four cells, the **spermatids**. Each spermatid elongates, and finally becomes a sper-

matozoon, consisting of a head, containing the nucleus, and an elongated cytoplasmic tail which projects into the lumen of the tubule. When the spermatozoa are mature, they become detached from the wall of the tubule and pass to the surface by the reproductive duct.

Oogenesis occurs either in the ovary, or shortly after the egg-mother-cell has left the ovary. It agrees, in cytological details, with spermatogenesis, but differs in that but one fertile female gamete is formed from the mother-cell. The ovary produces egg-mother-cells, or *oocytes*, with diploid nuclei. The oocyte nucleus divides into two, during which the number of chromosomes is halved. Of the two haploid nuclei resulting, one receives a small amount of cytoplasm and is gradually extruded, as the *first polar body*, to the surface of the larger cell. A second nuclear division now takes place, so that the larger cell extrudes a *second polar body*, whilst the first polar body may have formed two smaller cells. The nucleus remaining in the main part of the cytoplasm of the oocyte is the fertile female nucleus, which, together with the cytoplasm, forms the ovum. The significance of the behaviour of the oocyte nucleus is that the haploid chromosome number has been established. In this case, however, the result of the reduction division is not the production of four fertile gametes, as in spermatogenesis, but one fertile ovum and three (or two) vestigial cells with no further function.

The ovum of most animals includes a supply of food, known as *yolk*, which varies in quantity in different animals. The eggs of mammals, and those of many lower animals, contain little yolk and are described as *microlecithal*, whilst those of the frog and the birds contain a large amount and are said to be *telolecithal*. The yolk of telolecithal eggs collects at the lower side, remote from the nucleus, so that the *vegetative pole* is distinguished from the upper *animal pole* which consists of a clear cytoplasm in which the nucleus is situated. It will be seen, later, that the amount of yolk present influences the future development of the egg.

Subsequent to the formation of gametes, fertilisation occurs. In the frog the entry of the spermatozoon into the egg takes place immediately after the emergence of the eggs from the body of the female. A spermatozoon enters an egg and the cytoplasm of the two become mingled, whilst the gamete nuclei, now known as the *male* and *female pro-nuclei* respectively, lie close together. A nuclear spindle is formed from a centrosome originating in the spermatozoon, and the pro-nuclei each produce an equal number of chromosomes. These chromosomes become arranged at the equator of the spindle, prior to their longitudinal division in a

normal mitotic manner. In this way the zygote nucleus comes to possess the diploid number of chromosomes which is maintained in all subsequent nuclear divisions, until germ cells are once again formed.

In addition to restoring the full complement of chromosomes, fertilisation *activates* the egg, stimulating it to commence cell-division to form a new animal. The factors involved in activation are not fully understood, for it is found that the egg-cells of some animals will divide without the entry of a spermatozoon. When this occurs it is called *parthenogenesis*, a common event in certain insects, including the Aphides, and in plants of the family Compositæ. The eggs of the hive bee may be fertilised or may develop parthenogenetically, but in the former case the resultant insects are females, or 'worker' bees, whilst in the latter, they are males, or 'drones.' Parthenogenesis can be induced artificially in the eggs of the sea-urchin, frog and other animals, by both mechanical and chemical means, but the animals produced develop only as far as the larval stage. Artificial stimulants include pricking with a needle, raising the temperature, and immersing the eggs in various solutions.

The sex of the animal resulting from fertilisation is determined by the chromosome constitution of the gametes involved in fertilisation, for though the chromosomes taking part in gametogenesis have been previously considered as pairing equally prior to the reduction division, this is not strictly true. In mammals and many insects the cells of the female parent differ from those of the male parent with regard to chromosome structure. The female somatic cell contains two *sex*-, or X-chromosomes, which pair in the meiotic division during oogenesis, so that the surviving ovum will always contain an X-chromosome. The male somatic cell, on the other hand, contains a single X-chromosome, which may be paired, in meiosis, with a dissimilar Y-chromosome, so that, as a result of spermatogenesis, 50 per cent of the male gametes possess an X-chromosome and 50 per cent do not. Therefore, on fertilisation, two re-combinations are possible, viz. a zygote with two X-chromosomes, or one with a single X-chromosome. It is clear that the organism arising from the development of the former will be female, and from the latter, male.

In most birds, and some insects, this condition is reversed, the male possessing two X-chromosomes, and the female only one. In this case the male gamete always contains an X-chromosome, but the female may not. When the two X-chromosomes are restored in fertilisation, a male will result, but if the zygote contains but one X-chromosome a female will develop.

The early development of the fertilised egg follows the same plan in all animals, although appearances may be modified by the quantity of yolk present.

The process is called *segmentation*, which consists, essentially, of *cleavage*, or division of the egg into a number of smaller cells, or *blastomeres*, unaccompanied by an immediate increase in size. Eggs with little or no yolk cleave, more or less, equally; those with a certain amount of yolk cleave completely but give rise to small upper cells and larger lower cells containing yolk, whilst eggs, containing a considerable quantity of yolk, cleave incompletely, and confine the divisions to a small plate of cells, at the upper animal pole, lying on a large mass of yolk. It is, therefore, possible to distinguish complete, or *holoblastic* segmentation, which may be *equal*, as in the sea-urchin (Fig. 188), or *unequal*, as in the frog (Fig. 189), and partial or *meroblastic* segmentation, as in the chick. The first result of cleavage is the

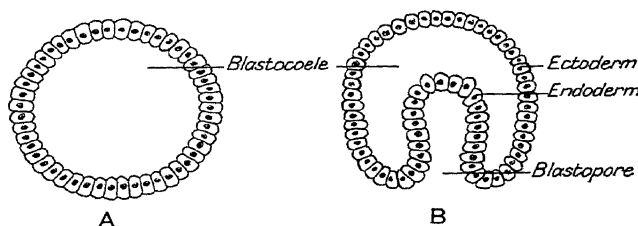


FIG. 188.—Development of a Sea Urchin.

A, section of Blastula; B, section of Gastrula.

formation of a hollow sphere of cells, the *blastula*, which encloses a central cavity or *blastocoele*. In holoblastic segmentation, the blastocoele appears early, and enlarges as the division of the surrounding cells proceeds, but in meroblastic segmentation the blastocoele is much less obvious and is represented by a narrow space between the disc of cells above the yolk. The subsequent development of the blastula depends on the animal, but the general procedure in triploblastic animals involves such foldings as will give rise to the three fundamental embryonic layers,¹ *ectoderm*, *mesoderm* and *endoderm*. The folding invariably commences with a stage called the *gastrula*, which may be produced in various ways, but in its simplest form consists of an invagination, or growing in of the wall, of the blastula.

This occurs in the sea-urchin (Fig. 188), the blastula of which is formed by holoblastic segmentation. The lower side of the blastula commences to flatten, and enters the blastocoele until it

¹ Also known as epiblast, mesoblast and hypoblast respectively.

arrives against the other side. This causes a second cavity to be formed, which communicates with the exterior by a small hole, the **blastopore**. The cavity is the **archenteron**, or primitive gut, which is lined by the endoderm formed by the ingrowing cells. The outer layer, or ectoderm, of the gastrula consists of the original outer layer of the blastula. As gastrulation proceeds, the

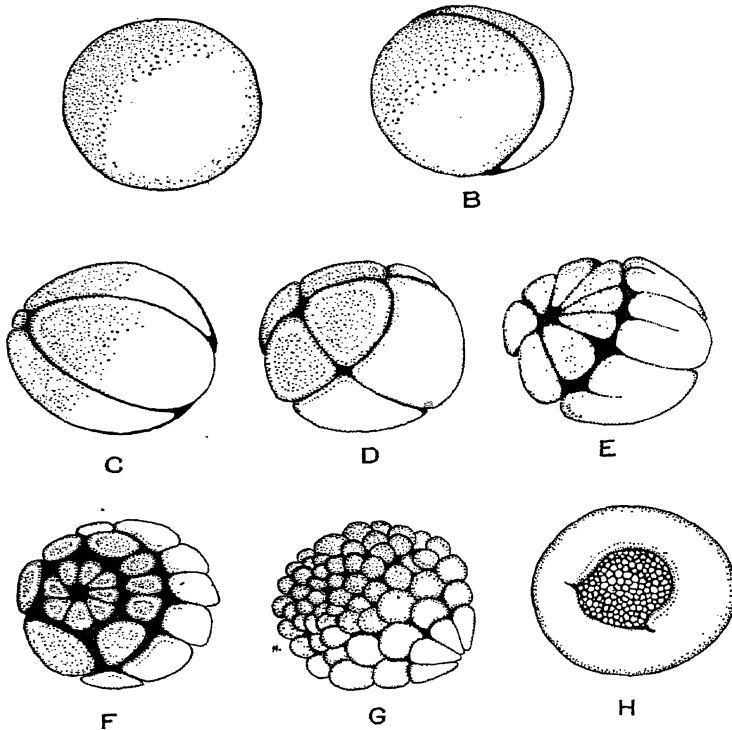


FIG. 189.—Segmentation of the Frog's egg.

A, undivided egg; B, first vertical division; C, second vertical division; D, first transverse division; E-G, development of blastula; H, epiboly has proceeded, and the blastopore is forming.

archenteron becomes deeper, and later the third germinal layer, the mesoderm, arises by the division of certain cells of the inner endoderm. The three germinal layers, so established, develop in various ways to form the organs of the animal.

The Embryology of the Frog (Figs. 189-193)

The egg, when laid, is a small spherical body with a whitish vegetative pole, and a black animal pole in which the nucleus is

situated. The first polar body was extruded before the egg left the female's body, but the second polar body is not extruded until the entry of a spermatozoon. When the egg has been fertilised

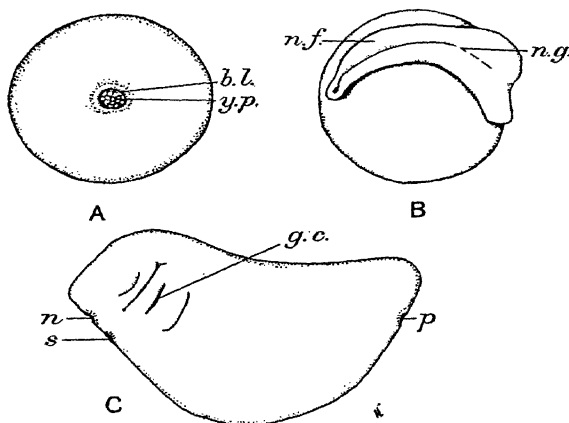


FIG. 190.—The development of the Frog.

A, Gastrula; B, formation of neural groove; C, an older embryo.

(*b.l.* = lip of blastopore, *g.c.* = visceral arch, *n* = beginning of nasal capsule, *n.f.* = neural fold, *n.g.* = neural groove, *p* = proctodæum, *s* = stomodæum, *y.p.* = yolk-plug.)

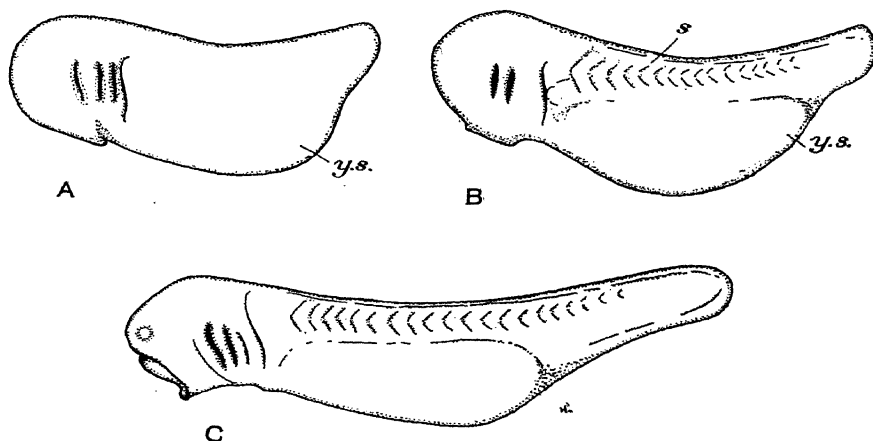


FIG. 191.—Later stages in the development of the Frog (enlarged).

(*s* = somite, *y.s.* = yolk sac.)

it is surrounded by a delicate *vitelline membrane*, and rotates, so that the vegetative pole is below. The gelatinous coating surrounding the egg swells when the egg reaches the water.

Development proceeds at once, and cleavage is holoblastic. By two divisions in the vertical plane and one at right angles to them an eight-celled embryo is formed, but owing to the yolk present, the blastomeres are unequal and consist of four small upper cells, or *micromeres*, and four lower larger cells, or *megameres* (Fig. 189, D). Cell-division continues at both poles, but cleavage is slower at the vegetative pole, as the yolk hinders division. A blastula is eventually formed, the wall of which is composed of numerous small upper cells and a smaller number of larger lower cells (Fig. 189, G). A blastocoele is formed inside, but it remains small

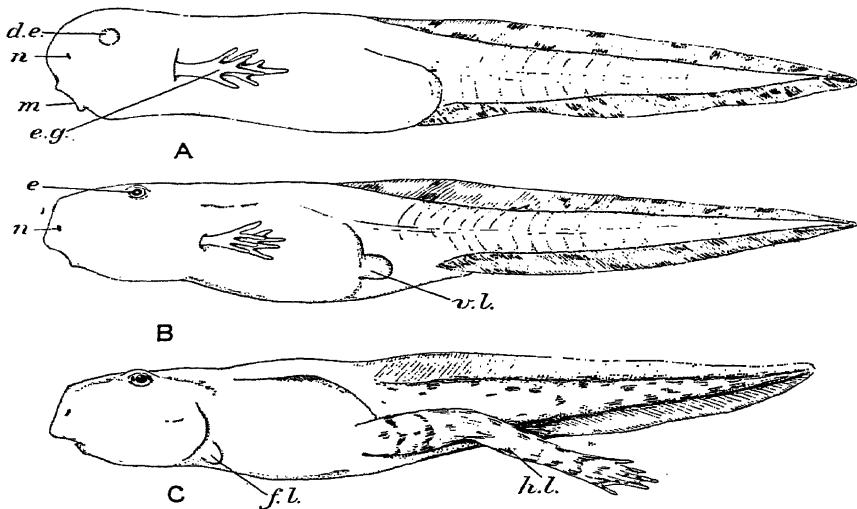


FIG. 192.—Late stages in the development of the Frog (enlarged).
(*d.e.* = developing eye, *e* = eye, *e.g.* = external gill, *f.l.* = origin of fore-limb, *h.l.* = hind-limb, *m* = mouth, *n* = nostril, *v.l.* = origin of hind-limb.)

and almost entirely confined to the animal pole. The cells of the animal pole now divide by tangential walls which results in the upper wall of the blastula becoming several cells thick, after which gastrulation commences. Owing to the presence of yolk, gastrulation cannot take place by a simple invagination but begins by the upper cells dividing and growing down towards the vegetative pole. In this way the upper, or ectoderm cells, cover the lower megameres, a process described as *epiboly* (Fig. 189, H). The ectoderm cells are pigmented, so that as epiboly proceeds, the egg appears black externally. The overgrowth of the pigmented cells is not uniform over the whole surface, as at one point the cells grow inwards forming the *blastopore lip*. The final result is to leave a lower white spot, the blastopore,

which is filled with a plug of cells, the **yolk plug** (Fig. 190, A). Rapid cell-division takes place at the lip of the blastopore to form a layer of cells, the endoderm, which extends inwards, parallel to the surface. The endoderm forms more rapidly on the future dorsal side, and its formation is assisted elsewhere by the differentiation of certain yolk cells. This stage in the development of the embryo is the two-layered gastrula, which consists of an outer ectoderm and an inner primitive endoderm.

Whilst gastrulation has been going on, the alimentary canal has

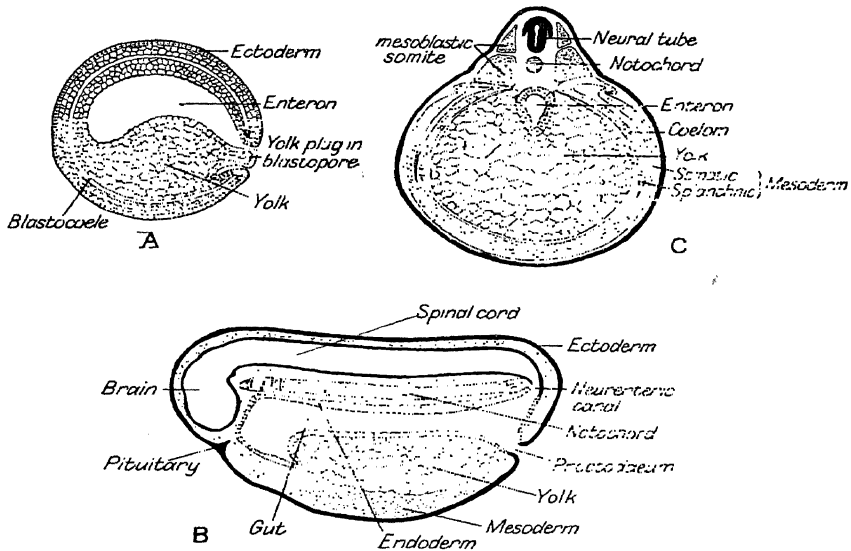


FIG. 193.—Development of the Frog.

A, longitudinal section through egg in the late gastrula stage; B, median longitudinal section through the embryo, shortly before hatching; C, transverse section of embryo in vertical plane (all diagrammatic, and much enlarged).

commenced to develop as a cleft, the **archenteron**, between the endoderm and the yolk cells, near the blastopore (Fig. 193, A). This cleft extends dorsally and dilates in the sphere, causing first a diminution in the size of the blastocoele, and finally, its complete obliteration. The yolk plug shrinks inwards and causes the blastopore to become slit-like. The blastopore marks the posterior end of the future animal, and, about this time, the egg rotates to bring it into the correct position in the horizontal plane. Within the gastrula there is still a quantity of yolk which forms the lining of the lower border of the enteron. The enteron is lined at other points by the endoderm. After rotation, the egg commences to elongate,

but the mesoderm has been formed before the completion of gastrulation. The mesoderm is formed partly by cells which are budded off by the blastopore lip and pass inwards between the ectoderm and endoderm, and partly by cells formed by the differentiation of the yolk cells lying between the ectoderm and the endoderm. The mesoderm, eventually, extends as a complete layer around the embryo, with the exception of a region in the mid-dorsal line, occupied by the notochord. It is, at first, a layer of several cells, but splits later to form a cavity which becomes the coelom. The layer of mesoderm surrounding the enteron is the *splanchnic* layer, and that beneath the ectoderm, the *somatic* layer (Fig. 193, c).

From the three embryonic layers now present, the tissues of the body arise. The ectoderm is concerned with the formation of the epidermis and its associated glands, the whole of the nervous system and sense organs, and the pituitary and pineal bodies. The endoderm gives rise to the epithelium lining the alimentary canal and those structures arising as outgrowths from it, such as lungs, and the bladder. The mesoderm produces the tissues between the epidermis and the lining of the alimentary canal (with the exception of those tissues already mentioned), the skeletal and muscular tissues, and the reproductive, excretory and vascular systems.

As the elongation of the embryo proceeds, the central nervous system and the notochord are formed.

The notochord, serving to support the embryo, arises from cells along the dorsal side of the enteron. The central nervous system is formed dorsally from a median ectodermal plate. At first it takes the form of a flattened *neural plate* which is broader at the anterior end where the brain will be formed. Ridges appear at the sides of the neural plate, giving rise to the *neural folds* which produce a longitudinal *neural groove* in the middle line (Fig. 190, B). The neural groove deepens by further upgrowth of the folds which finally meet and fuse—to form the *neural tube*. The neural tube is closed in front, but at the hinder end it remains in communication with the enteron by a short *neurenteric canal* (Fig. 193, B), which closes before the tadpole is hatched. The walls of the neural tube undergo thickening, and, by further changes, the tube becomes differentiated into the brain and the spinal cord. The eyes are formed later by a pair of lateral outgrowths extending from the brain towards the ectoderm. These outgrowths become concave at their free ends, to form the *optic cups*, and from the ectoderm overlying the optic cups, the lenses of the eyes are formed. The dorsal region of the mesoderm, on either side of the nerve-cord and notochord, becomes segmented to produce a

longitudinal series of *mesoblastic somites*, which later on are concerned with the formation of the *myotomes*, or muscle segments, of the body wall.

During the time that the neural plate is developing into the neural canal, lateral *gill-plates* and *sense plates* arise at each side of its anterior end.

The alimentary canal, produced by the enteron, is cut off from the exterior when the blastopore closes. The closing of the canal is temporary, for, at the posterior end of the embryo, ventral to the position of the blastopore, the ectoderm infolds to form the *proctodæum*, which ultimately meets the endodermal part of the canal (Fig. 193, B). A similar invagination, the *stomodæum*, forms at the anterior end to complete the canal. The stomodæum forms the buccal cavity, and the proctodæum forms the cloaca.

The lungs arise as a bilobed outgrowth on the ventral side of the alimentary canal, behind the buccal cavity, and, at the posterior ventral side of the canal, the bladder is formed by a similar outgrowth.

Before the tadpole hatches, each gill-plate produces grooves which mark the positions of the *visceral arches*, and from the first two pairs branched *external gills* arise. A curved sucker is formed behind the stomodæum, and above it, in each of the sense plates, an olfactory organ arises as a small pit.

The vascular system commences beneath the pharynx as a straight tube of mesodermal origin, which becomes the heart and its associated sinus venosus. The blood-vessels develop in various ways, in close communication with the gills, for in its early stages the tadpole has a circulatory system similar to that of a fish.

When the tadpole hatches, leaving the gelatinous coating of the egg, more changes take place in its structure. Another pair of external gills are formed, and the mouth is provided with a pair of horny jaws. Four pairs of gill-slits open, on which the external gills shrivel and disappear, being replaced by *internal gills* on the sides of the slits, which become protected by folds of skin, the *opercula*, growing backwards from the sides of the head.

On assuming a free existence, the tadpole feeds on materials in the water, and continues to enlarge. Metamorphosis (Fig. 192) gradually takes place, during which changes occur in the vascular system, limbs develop, and the tail disappears, so that finally a frog is produced.

The Embryology of the Chick (Figs. 194-200)

The egg of the hen consists of a single cell which is much enlarged because of the presence of a large quantity of yolk. The

clear rotoplasm, which includes the nucleus, forms a small **germinal disc** at the animal pole. The egg is liberated from the and the first polar body is extruded as the egg enters the

Fertilisation takes place high up in the oviduct, the a having been introduced into the cloaca by the male. some polar body is extruded immediately prior to the fusion sperm nucleus with that of the egg.

fertilisation, the egg passes down the oviduct and receives

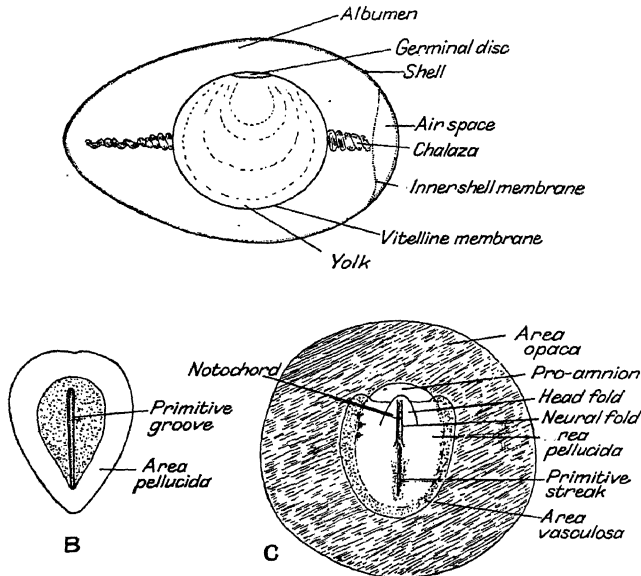


FIG. 194.—Development of the Chick.

A, median longitudinal section through the fowl's egg ; B, surface view of part of blastoderm, 12 hours after incubation ; C, the same, about 20 hours after incubation.

various coatings from glands associated with the oviducal wall. The first coat is a viscous layer of albumen which, owing to the rotation of the egg, becomes coiled at either end to form two tough threads, the **chalazæ**. A more fluid layer of albumen is then deposited, followed by inner and outer parchment-like shell-membranes, and an outer chalky shell. An air-space is left between the inner and outer membranes, at the blunter end of the 'egg' (Fig. 194, A).

The development of the egg commences during its passage down the oviduct, and, owing to the quantity of yolk, segmentation is

meroblastic. The protoplasm of the animal pole divides to form a plate of cells, the **blastoderm**, no division occurring in the yolk. Except at the periphery, a cavity, the blastocœle, separates an upper layer of cells from a lower layer which is closely applied to the yolk. This stage corresponds to the blastula of the frog. The lower layer of cells, the endoderm, separates from the underlying yolk, so forming a **sub-germinal cavity** which is equivalent to the archenteron of the frog.

Gastrulation takes place by a process called **delamination**. Small cells are split off, from the underside of the blastoderm, to form a somewhat irregular layer which is continuous at the periphery, with the upper layer. The egg is laid at this stage, about 24 hours after fertilisation.

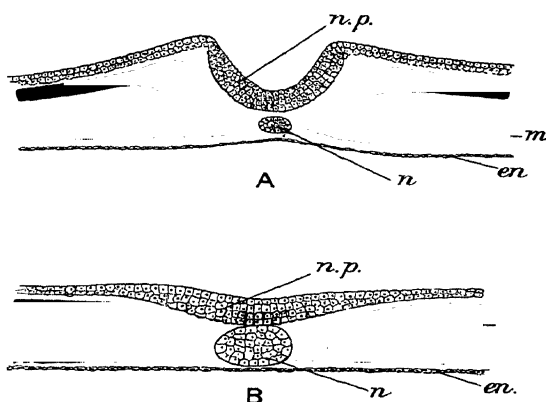


FIG. 195.—Diagrammatic transverse sections through the blastoderm of the Chick, about 24 hours after the commencement of incubation.

A, anterior region; B, posterior region (the yolk lies beneath the endoderm).

(en. = endoderm, m = mesoderm, n.p. = neural (medullary) plate of ectoderm.)

After leaving the body of the mother the egg must be maintained at a temperature of 37° to 40° C., or further development is arrested.

Under satisfactory conditions of incubation, the blastoderm spreads over the upper surface of the egg. The upper and lower layers of cells (ectoderm and endoderm respectively), are thicker at the periphery than elsewhere, so that by transmitted light the blastoderm presents two zones. The inner clear zone is the **area pellucida**, and the outer denser zone, the **area opaca**.

In the middle of the area pellucida, the ectoderm thickens and elongates at right angles to the long axis of the 'egg,' forming the **primitive streak** (Fig. 194, B), which, together with a small portion

of the tissue directly beneath it, represents the true embryo. The other tissues which develop are described as *extra-embryonic*. The primitive streak is comparable with the fused blastopore lips of the frog embryo, but the actual aperture of the blastopore is represented by the *primitive groove*, and a slight depression, the *primitive pit*, at the anterior end of the primitive streak. The primitive groove is a longitudinal furrow in the middle line of the primitive streak.

The primitive streak, which is the region of active growth, cuts off mesoderm cells which spread laterally between the ectoderm

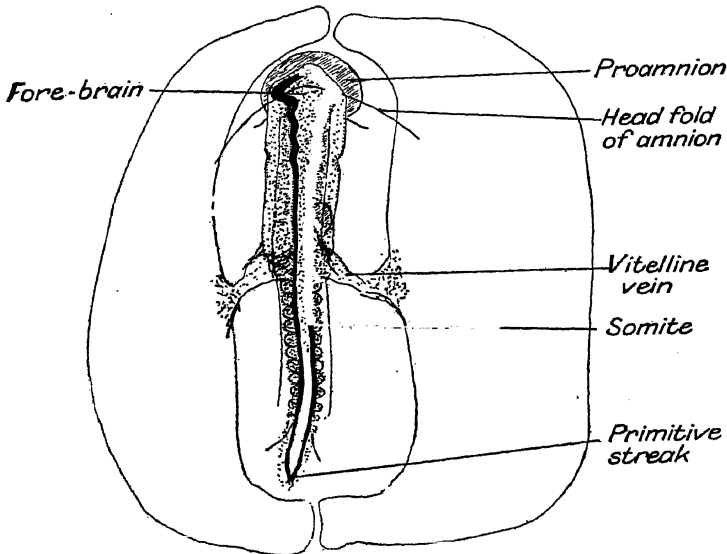


FIG. 196.—Embryo of the Chick, about 36 hours old, seen from above (enlarged).

and endoderm. The primitive streak continues backwards, leaving, in its wake, a line of cells which later become the notochord.

The blastoderm extends over the surface of the egg to enclose the yolk, and as the formation of ectoderm, mesoderm and endoderm follows, the endoderm encloses the yolk mass, now called the *yolk-sac*.

The mesoderm extends equally in the posterior and lateral directions, but in the anterior region it grows forward as a pair of lateral extensions which eventually unite. Therefore, for a time, there is an area, the *pro-amnion* (Fig. 194, c), formed from ectoderm and endoderm only, in front of the embryo. A neural plate

(Fig. 195) develops as a median thickening of the ectoderm in front of the primitive streak, and extends with the primitive streak as it moves backwards. Neural folds arise at the sides of the neural plate, and meet dorsally to form a neural tube. The anterior end of the neural tube is enlarged, and becomes divided by constrictions into the three regions of the rudimentary brain (Fig. 200, Δ).

The eye develops as a lateral outgrowth of the forebrain, its development, including the formation of the lens, being similar to

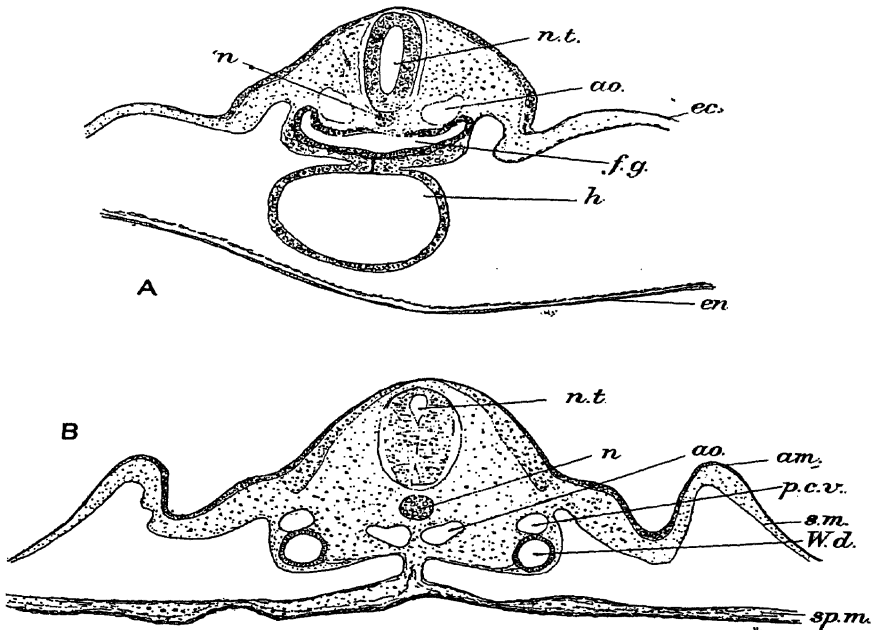


FIG. 197.—Transverse sections through a Chick embryo, about 48 hours old.

A, in the heart region; B, in trunk region, with side folds of amnion arising.

(*am.* = amnion fold, *ao.* = aorta, *ec.* = ectoderm, *en.* = endoderm, *f.g.* = anterior part of gut, *h* = heart, *n* = notochord, *n.t.* = neural tube, *p.c.v.* = posterior cardinal vein, *s.m.* = somatic mesoderm, *sp.m.* = splanchnic mesoderm, *W.d.* = Wolffian duct.)

that of the frog. The ears develop as ectodermal ingrowths in the region of the hind-brain.

The mesoderm becomes divided into somites (Fig. 196), of which the parts nearest the notochord produce myotomes, whilst the lateral parts split to form the coelomic cavity. The cavity is bounded by *somatic mesoderm*, applied to the ectoderm, and *splanchnic mesoderm* next to the endoderm (Fig. 197). A coelomic cavity is formed in a similar manner in the extra-embryonic tissues, and this is called the *extra-embryonic coelom*.

A crescentic *amnionic fold* arises from the extra-embryonic tissues at the anterior end of the embryo (Fig. 200, A). This fold is, at first, composed of ectoderm only, as the mesoderm has not yet spread into the pro-amnionic region. It continues backwards and laterally around the embryo, the posterior and lateral folds consisting of ectoderm and somatic mesoderm (Fig. 197, B). The folds eventually fuse so as to enclose the embryo in a cavity filled with fluid which protects the embryo from mechanical shock and helps to maintain an even temperature. The cavity possesses a double

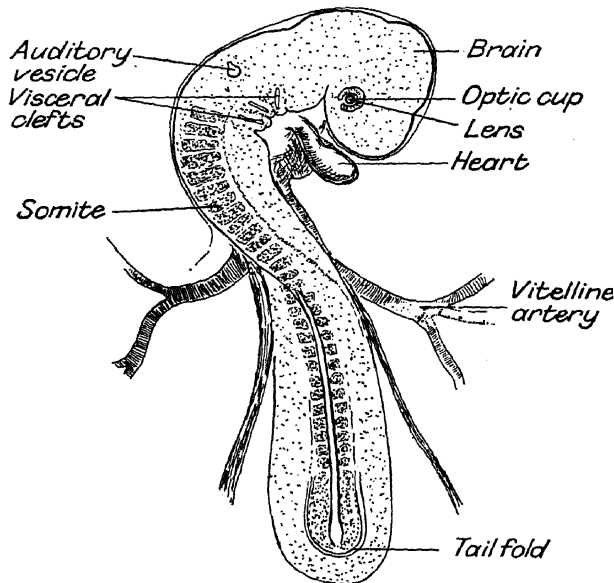


FIG. 198.—Embryo of Chick, about 60 hours old, viewed from above—note the cranial flexure.

wall, of which the inner is formed externally from mesoderm and internally from ectoderm, and is the *true amnion*, one of the *foetal membranes*. The true amnion is separated, by part of the extra-embryonic coelom, from the second wall of the cavity, formed externally of ectoderm and internally of mesoderm, which is the *false amnion* or *chorion* (Fig. 199). The embryo has by this time commenced to fold off from the yolk-sac, by the amnion growing in beneath the embryo. At the anterior and posterior ends, the ectodermal lining of the amnion and the ectoderm around the embryo grow inwards to form the anterior and posterior regions of the alimentary canal, viz. stomodæum and proctodæum respec-

tively. The middle portion of the canal is lined by endoderm, but, as yet, has no floor, as it is still connected with the yolk-sac. The connection becomes progressively narrower, however, until finally, a thin connecting stalk, the *umbilicus*, remains (Fig. 200, B).

The food contained in the yolk-sac is absorbed and passed to the embryo by means of *vitelline veins*.

At about this stage of development, the head twists so as to lie with the left side against the yolk-sac, and the right side towards the shell, a condition known as *cranial flexure* (Fig. 198). At a later stage the entire embryo turns on its left side, and shortly before hatching turns so as to lie along the long axis of the egg, with its head towards the larger end. Another foetal membrane, the *allantois* (Fig. 200, B), commences as a downgrowth of the floor

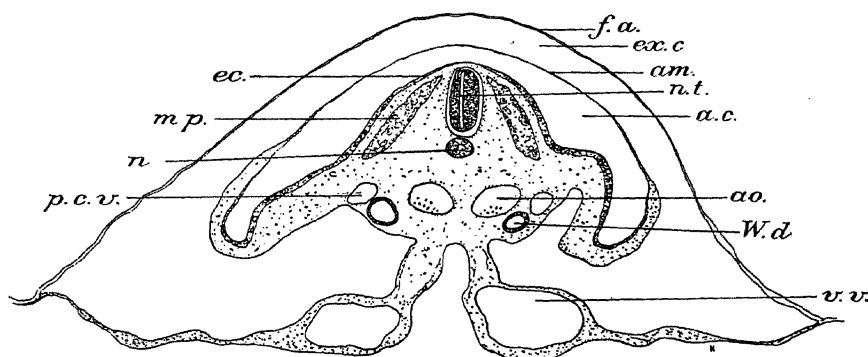


FIG. 199.—Transverse section through the trunk region of the embryo of a Chick, about 3 days old.

(a.c. = amniotic cavity, am. = amnion, ao. = aorta, ec. = ectoderm, ex.c. = extra-embryonic coelom, f.a. = chorion, m.p. = muscle plate, n = notochord, n.t. = neural tube, p.c.v. = posterior cardinal vein, v.v. = vitelline vein, W.d. = Wolffian duct.)

of the posterior part of the alimentary canal, forming a sac lined by endoderm and with an external layer of splanchnic mesoderm. The allantois increases in size, as development continues, and grows up into the extra-coelomic space, between the amnion and false amnion. The mesoderm surrounding the allantois fuses with that associated with the amnion and false amnion, and so the allantois becomes closely applied to the shell membranes. The main functions of the allantois are respiratory and excretory. The organ is richly supplied with blood-vessels, and gaseous exchanges with the atmosphere can readily occur through the porous shell and the shell membranes. It is also concerned with the removal of the waste matter produced by the embryo, which is passed to the allantois, where it remains.

In the neck region of the embryo, three or four pairs of gill-clefts develop which do not bear gills, but are in communication with the amnionic cavity. The heart is formed by part of a median blood-vessel, running beneath the floor of the anterior part of the

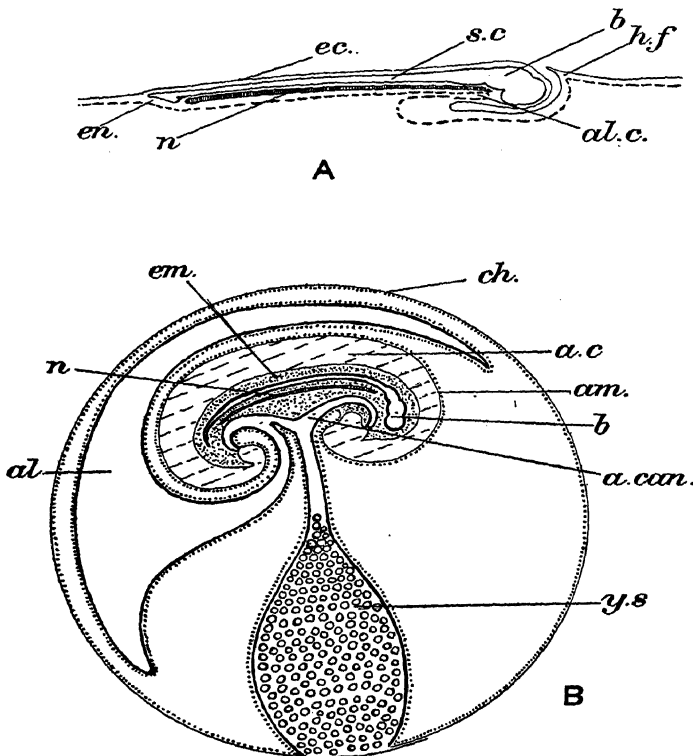


FIG. 200.—Development of the Chick.

A, median longitudinal section of embryo, about 30 hours after incubation; B, diagrammatic longitudinal section through the egg to show the foetal membranes (ectoderm = thin continuous line, endoderm = thick continuous line, mesoderm = dotted line).

(*a.c.* = amnionic cavity, *a.can.* = alimentary canal of embryo, *al.* = allantois, *al.c.* = beginning of fore-gut, *am.* = amnion, *b* = brain, *ch.* = chorion (false amnion), *ec.* = ectoderm, *em.* = embryo, *en.* = endoderm, *h.f.* = head fold of amnion, *n* = notochord, *s.c.* = spinal cord, *y.s.* = yolk sac.)

gut, formed by the union of a pair of vitelline veins from the yolk-sac (Fig. 198). The vascular system of the embryo, at this stage, resembles that of a fish, consisting of a number of paired vessels passing anteriorly in front of the heart.

The various other organs of the body have meanwhile been developing, and after some twenty days of incubation, the young chick is ready to emerge from the egg.

The lungs have been formed, and changes in the vascular system have occurred to enable these to be used as respiratory organs. Immediately prior to hatching, the yolk-sac is absorbed within the body, the allantois continuing to function until the lungs are inflated. The chick pierces the air-space between the membranes at the broad end of the 'egg,' and inflates its lungs with the contained air. The allantois now shrivels and is detached by fracture of the umbilicus. The beak of the chick bears a sharp projection which is used to break the outer shell, on which the active chick escapes to a free life.

CHAPTER XXIX

EVOLUTION. THE MECHANISM OF EVOLUTION. HEREDITY

It was stated in the introductory chapter that it is now generally accepted that the higher forms of life have developed gradually, or evolved, from simpler ancestors. A survey of the existing life of the world may help to support this view, for evolution does not necessarily mean a complete transformation of ancestral forms, but rather a gradual production of new types by some of the offspring. In some cases the simpler ancestral types have survived unaltered to the present day. This is evidenced by a simple group of widely distributed Algæ, the Diatoms, which occur as fossils in certain beds of siliceous earth in various parts of the world, as well as being distributed in the present flora. Fossil diatoms are almost indistinguishable from the living members of the group.

Nothing is known about the origin of living matter, but it can be assumed to have occurred millions of years ago. The age of the earth has been calculated to be at least one thousand million years, and life has existed for at least half that period.

Organic evolution is a slow process, and no evidence of its occurrence is to be expected in a lifetime, nor over a much longer period. It would appear, however, that in the history of the earth, there were certain eras during which evolutionary progress was accelerated, and, presumably, such eras may occur in the future. Evidence of evolution has been obtained from a number of sources, particularly the geological record, geographical distribution, comparative morphology and embryology.

Geological Evidence.

The earth's crust is composed of rocks, many of which were formed by sedimentation, or the deposition of mineral matter on the sea-bed, at the mouths of rivers, and in inland lakes. In many parts of the world the beds of rock are arranged in their correct order as regards age of deposit. During the formation of the sedimentary rocks, dead plants and animals become covered with silt and their bodies have been preserved as *fossils* in the rocks. In many cases only the harder parts of the organism have been pre-

served, such as the bones and teeth of animals, and the woody trunks of plants. In some instances the cellular structure has been preserved by the infiltration of the cell-walls with mineral matter, so that by special technique the microscopical appearance of the tissues may be ascertained. From the study of fossils it is possible to gain some idea of the forms of life which formerly inhabited the earth, and in cases where fossil-bearing rocks are conformably arranged, evidence may be obtained of the evolutionary changes which were going on. From the fossil record it is proved that the ancient faunas and floras of the world differed from those now existing, but that they included the ancestors of some of the modern forms.

Little satisfactory evidence of plant evolution is available from the fossil record, as the softer tissues of plants are not suitable material for preservation. Nevertheless, many fossil plants have been discovered and from them it is known that the Pteridophyta had an extensive distribution over the earth at a time when few Seed-plants were in existence. It is also known that in the geological period called the Coal Measures, certain plants, the Pteridosperms, now extinct, appeared to combine the characters of the Pteridophyta and the Seed-plants. The fossil record also shows that the Pteridophyte groups, the Horsetails and the Clubmosses, at present represented by a few herbaceous plants, consisted of tree-like members with secondary growth. This helps to confirm the view that herbaceous plants are derived from woody ancestors, for which reason the Gymnospermæ, composed entirely of woody plants, is considered more primitive than the Angiospermæ which includes herbaceous forms. The Gymnosperms, incidentally, have the older fossil record, suggesting their earlier evolution.

Evidence of the evolution of a number of animal groups is more satisfactory, as they are represented in the fossil record by types which exhibit the relatively small changes required by a theory of evolution.

The modern horse (*Equus*) is represented by a number of transitional forms which suggests its origin from a four-toed ancestor, *Hyracotherium*,¹ a small animal of the geological period called the Eocene. *Hyracotherium* probably walked on the sole of its foot, like a dog, but its descendants gradually acquired the habit of walking on the end of one digit, so that the remaining toes degenerated. The hoof of the modern horse is the 'nail' of this

¹ *Hyracotherium* appears to have originated in Western Europe, and gave rise to a very similar descendant, *Eohippus*, which migrated to North America, by way of Asia, and became the direct ancestor of the forms which culminated in the horse.

surviving toe, the other toes being represented by 'splint-bones' in the hock (Fig. 201).

The elephant (*Elephas*) has apparently evolved from a small Eocene animal *Mœritherium*, which possessed normal jaws having more or less typical dentition. Descendants of the animal developed

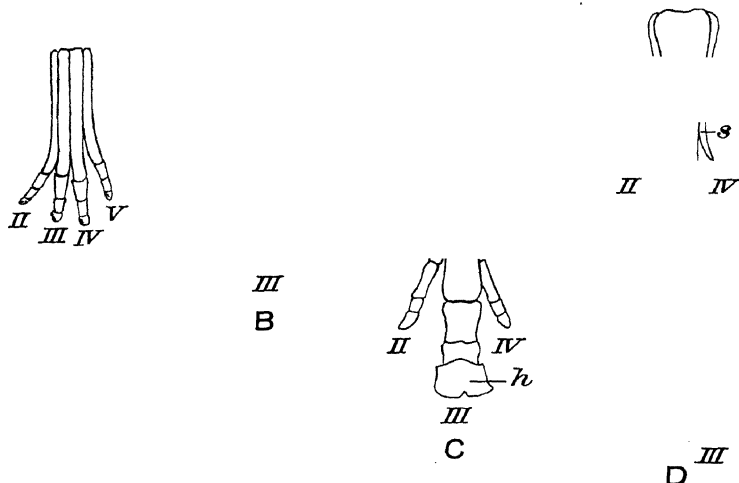


FIG. 201.—Stages in the evolution of the fore-foot of the Horse.
 A, *Hyracotherium* (Eocene period); B, *Meshippus* (Oligocene period); C, *Merychippus* (Miocene period); D, *Equus* (Present).
 (Numerals refer to digits of pentadactyl limb.)
 (h = hoof (nail of third digit), s = splint-bone.)

unusual jaws and pronounced incisor teeth, until the modern elephant arose with a shortened lower jaw and an upper jaw bearing a pair of large incisor teeth, the tusks (Fig. 202). Other changes which were involved included the lengthening of the snout to form a trunk, and peculiarities in the bones of the skull.

Geographical Evidence.

The distribution of plants and animals in the world supports the view that organic evolution has occurred.

The chief factors which influence the distribution of a plant or an animal are its means of dispersal, and the accessibility of the area over which it might spread. Climate may play a part in geographical distribution, but the usual limitations to the spread of organisms are such natural barriers as oceans, deserts and mountain ranges. This is shown by the fact that animals like the sheep and the rabbit, which never occurred naturally in Australasia, have

spread rapidly and widely since they were introduced by man, showing that the conditions are quite suitable for their existence. The constitution of the fauna and flora of an isolated region depends on the period of isolation, and the proximity of the nearest land which could provide colonists. **Continental islands**, like the British Isles, are those which have quite recently become separated from the continent, which is not far distant, whereas **oceanic**

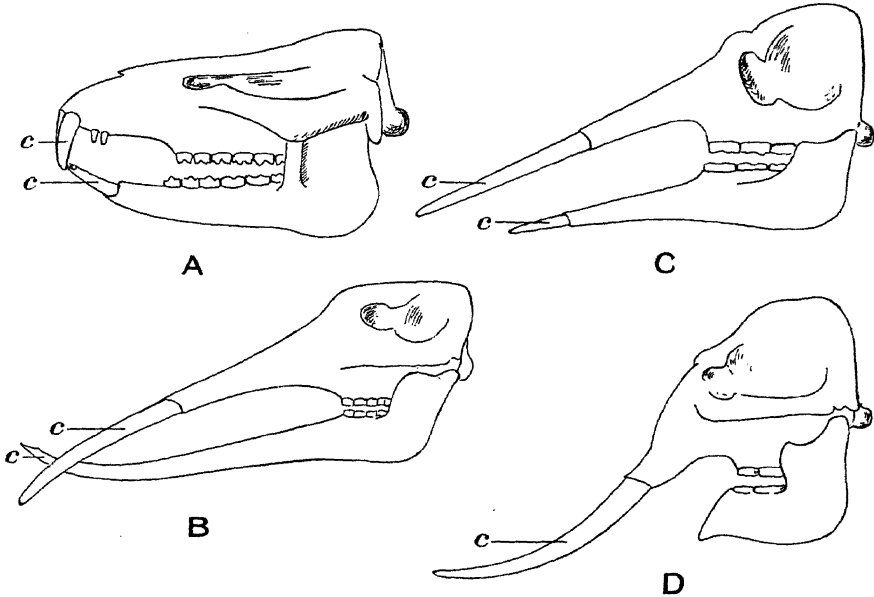


FIG. 202.—Stages in the evolution of the skull of the Elephant (not to same scale).

A, *Maeritherium* (Eocene period); B, *Tetrabelodon* (Miocene period type);

C, *Tetrabelodon* (Pliocene period type); D, *Elephas* (Present).

(c = incisor tooth.)

islands are separated from the nearest land by deep wide seas, and may have been isolated for a long period.

The population of continental islands agrees, in general, with that of the nearest land, as there has been little hindrance to the spread of species. On the other hand, the population of oceanic islands is found to include forms peculiar to the region (i.e. **endemic**), which is what might be expected if evolution goes on.

The fauna of Australia includes a number of animals peculiar to the continent, viz. marsupials, like the kangaroo and wombat, and a curious egg-laying mammal, the duckbill, and the flora includes

EVOLUTION

the genus *Eucalyptus*, which does not occur naturally elsewhere. Fossil evidence shows the marsupials to have formerly had a wider distribution than at present, including what is now modern Europe and Asia, and that they were not always restricted to the Southern Hemisphere. The suggested explanation is that the Australasian continent became separated from the Northern Hemisphere before the higher mammals had arisen, and, whereas in Eurasia the marsupials, and other lower forms, gradually succumbed to the spread of higher types, the absence of the latter from Australasia enabled the simpler mammals to spread and survive to the present day.

Charles Darwin obtained similar evidence of evolution from the oceanic Galapagos Islands, some 500 miles from the coast of South America. He found, for example, that certain plants were members of families and classes represented in South America, but the component species of the islands were almost entirely restricted to them. Twelve genera of the family Compositæ were present, of which ten were peculiar to the islands, and of the twenty-one species of these genera, twenty were endemic. The animal population showed a very similar state of affairs. The conclusion drawn is that the existing plants and animals of the islands are descendants of colonists from the mainland, but new species evolved along their own lines so that they no longer resemble their South American relatives.

Morphological Evidence.

On the basis of general characters, the known plants and animals can be grouped into large divisions, as has been suggested in previous chapters. A series of groups, showing an increasing complexity of structure, can be obtained, to indicate the possibility both of common origin and the development of multicellular from unicellular forms. There are, however, few types which provide the necessary connecting links between the various groups, although the Pteridophyta, such as *Selaginella*, suggest the origin of the Seed-plants, and show affinities, through their sexual organs, with the lower group, the Bryophyta. The similarities in the various life-cycles would be explicable on an evolutionary basis.

The limbs of the Vertebrates have been seen to be constructed on the same plan, which can hardly be considered to be a matter of chance.

Some animals possess anatomical structures which are no longer functional, but must be presumed to have had a use during the former history of the animal. Such *vestigial* structures may indicate a closer relation of animal types than would be gathered from general appearances. For example, the human backbone terminates with a curved structure, the coccyx, which is the sur-

living rudiment of an ancestral tail, and may be provided with the vestiges of caudal muscles, formerly concerned with the movement of the tail. The human appendix is vestigial and functionless, and a much smaller structure than that of a rabbit, for example. In some cases *atavism* occurs, in which a now-modified structure assumes a previous form. Instances are on record of human beings being born with small tails, and amongst plants, floral members frequently resume the leaf-like appearance they are believed to have formerly possessed.

The anatomy of birds and reptiles is very similar and suggests both close affinity and, perhaps, a common origin. This view is supported by the fact that both lay eggs, and their embryos are provided with amnion and allantois during development. The differences between the two groups include the body-covering, consisting of feathers in birds, and scales in reptiles, the almost complete absence of a tail from the birds, and the absence of teeth from the jaws of the birds. The fossil record has yielded a form, *Archæopteryx*, which combined, to some extent, the features of birds and reptiles, for it possessed true feathers, a long lizard-like tail, claws to the fore-limbs, which were wings, and well-developed teeth. *Archæopteryx* is practically the type which would be postulated if a link between birds and reptiles was being visualised.

Embryological Evidence.

The statement is frequently made that 'ontogeny repeats phylogeny.' This implies that the development of an organism indicates, to some extent, its evolutionary history, or phylogeny.

It is true that the normal life-cycles of plants and animals all

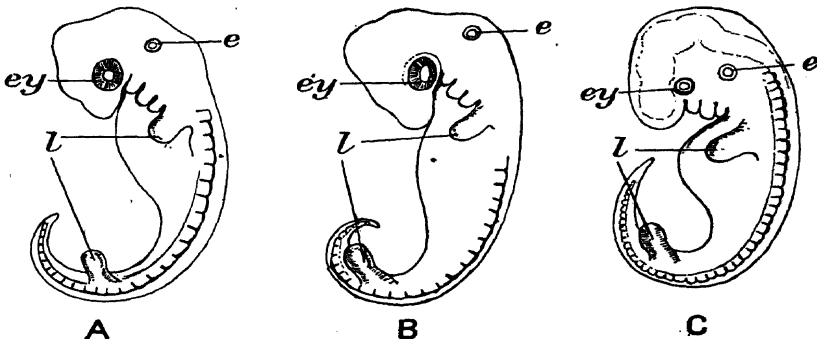


FIG. 203.—Diagrams of embryos at approximately the same stage of development, to show the similarity amongst reptiles, birds and mammals. (The foetal membranes and yolk-sacs have been removed.)

A, Tortoise; B, Chick; C, Rabbit.

(e = rudiment of ear, ey. = rudiment of eye, l. = rudiment of limb.)

commence with a single cell, similar to the unicellular organisms, and, by the development of this cell, a multicellular organism of considerable size and complexity may result.

During the development of all the higher animals, a two-layered blastula-stage is passed through, which is not unlike the body of the simple Coelenterates.

The embryos of reptiles, birds and mammals (Fig. 203), are so closely alike, during certain stages of their development, that they are not readily distinguished, which suggests a close affinity and a common ancestry. The embryo of the vascular plants is originally non-vascular, and the floral parts of Angiosperms originate in a very similar manner to the sporophylls of the Pteridophyta.

It can be realised, therefore, that the evidence from all sources is overwhelmingly in favour of the theory of evolution, although much has yet to be forthcoming to complete the story. The mechanisms which resulted in the changes required for evolution are not by any means clear, and have given rise to much conjecture.

Theories of Evolution

Lamarckism.

The French biologist, de Lamarck (1744–1829), noticed that animals of the same species were not identical, but showed slight variation. He developed a theory of the inheritance of acquired characters, which suggested that the organs of an animal might become modified, either through abnormal use, or disuse, and the resulting modification could be passed on to the offspring. For example, an animal, by reaching up for the foliage of tall trees, might cause its neck to grow longer. The increase in length would be inherited by the next generation, and by the process being repeated over several generations, an animal, like the giraffe, with an abnormally long neck, would arise.

This theory is particularly applied to animals, and at present has few supporters, as there is no satisfactory proof that, so-called, *acquired characters* are inheritable.

Darwinism.

Charles Darwin, in 1859, published an important work, *The Origin of Species*, which suggested the evolution of new species by a *natural selection*. Before considering the theory, the types of variation in organic nature must be considered. The offspring of a species are rarely exactly alike, but exhibit small variations, which are *continuous*, or *fluctuating variations*. They occur, for example, in plants, which may show slight differences in seed-size, floral parts, and so on, but the differences fluctuate about a mean type, which is always numerically superior to the others.

In some plants and animals, *discontinuous variations* appear, which are very marked, certain offspring differing considerably from the others and from the parent. This type of variation is known as a *mutation*, or *germinal variation*, and unlike the continuous variation, is inheritable. It is of common occurrence in the evening primrose (*Oenothera*), and in the fruit-fly (*Drosophila*).

Darwin appreciated the existence of variation in nature, and assumed that only germinal variations were effective. He considered the formation of offspring by animals and plants, and came to the conclusion that those of any individual could not all survive. The elephant, a notably slow-breeding animal, was instanced; it comes to maturity in about thirty years and produces one offspring in about ten years. Therefore, on the basis of breeding, it was calculated that in less than a thousand years, one pair of elephants could have given rise to nineteen million descendants. By similar calculations, and from the fact that the population of a particular species does not increase to the extent suggested, but remains more or less constant, Darwin concluded that some natural agency was at work. He believed that a struggle occurred, between species, for existence in an environment, and concluded that those forms best suited for continued existence would survive, and those unsuited would succumb. If, therefore, an individual possessed a variation favourable to survival, it would be perpetuated, as it would have advantages over the individuals lacking the variation.

Natural selection cannot be thought to play an important part in the evolution of new forms. It may be assumed to aid the removal of variations which are unsuitable, so limiting the competition of the better-suited forms, and probably serves to select and preserve the better individuals already in existence.

De Vries.

The theory of de Vries, a Dutch botanist, emphasises the importance of mutations, for the evolution of new species must be due to some factor which can alter the germinal structure of an organism. Mutations are known to occur which exhibit characters of favourable type, and, although many mutations are less suited to conditions and die off, it would seem that mutation combined with natural selection is a satisfactory explanation of the evolution of new organisms.

The Mechanism of Evolution

Theories of evolution do not suggest the whole method of transmission of characters to the offspring. This involves heredity, which is due to some component of the germ cells.

Chromosomes are characteristic of the vast majority of cells, and

their behaviour during cell-division suggests them to be concerned in the carriage of factors transmitting the hereditary characters. Weismann (1834–1914) pointed out that the reproduction of plants and animals was effected by *germ-cells* of different origin from the vegetative, or *somatic cells*, of the organism.

Chromosomes are now accepted as the transmitters of hereditary characters and are believed to contain *factors*, or *genes*, probably arranged as a longitudinal series of *chromomeres*. Each chromomere is concerned with the development of a particular factor, and those present in the germ-cells of *Drosophila* have been mapped out so accurately, that it is possible to explain the characters of the individual on the nature of its component chromosomes.

During mitosis in somatic cells, the daughter-nuclei receive the same set of factors because each chromosome divides longitudinally. In meiosis, which is the important nuclear division resulting in the formation of the reproductive cells, chromosomes become paired before division, and entire chromosomes separate in the heterotype phase. This results in the carriage, to one or other pole, of a complete set of factors, and the resultant germ-cells will depend, in character, on the chromosome structure of the original mother-cell.

The transmission of characters from parent to offspring was studied experimentally by an Austrian priest, Mendel, who published his results in 1865. These results received little notice at the time, and the facts were re-discovered independently by several investigators early in the present century.

Mendel is, however, credited with the discovery, and the science of breeding is generally referred to as *Mendelism*.

In his experiments, Mendel used the garden pea, because it was a quick-growing plant, it occurred in several varieties which bred true to the parental type, it was naturally self-pollinated, but could readily be cross-pollinated. He selected parents with contrasting features, such as tall and dwarf plants, plants with green seeds and with yellow seeds, and so on, each one of a pair of contrasting characters being called an *allelomorph*.

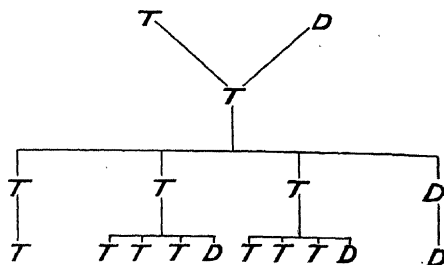
For example, he pollinated the flowers of a tall plant with pollen from a dwarf plant, and obtained the seeds which resulted. These seeds were planted, and the resulting plants all resembled one parent, in this case being tall. From the seeds produced by the self-pollination of this *hybrid*, he raised plants, and of these, 75 per cent were tall and 25 per cent were dwarf. When the seeds, produced by self-pollination of this generation, formed plants, it was found that the dwarf plants gave rise to dwarfs only, but of the tall plants, one-third produced tall plants, whilst two-thirds gave rise to tall and dwarf plants in the proportions previously occurring.

The results can be represented thus :

Parental generation (P)

1st Filial generation (F₁)

2nd Filial generation (F₂)



Mendel described the character which persisted in the F₁ generation, **Dominant**, and the character which was suppressed, **Recessive**.

He assumed that the characters were mixed in the hybrid generation, but that the unit characters segregated in the reproductive cells, which were to form the next generation. Thus a pollen grain of the F₁ plant would carry the character either for tallness, or for dwarfness, as would the ovules. On the basis of probability, as equal numbers of tall and dwarf gametes were formed, the zygotes resulting from self-pollination would have the constitution TT, TD, TD, DD. This would result in the production of the proportion of tall to dwarf plant obtained in the experiment.

The plants possessing the factor for tallness only, Mendel called **pure dominants**, and those also containing the suppressed factor for dwarfness, **impure dominants**. Actually there is no difference in external appearance between pure and impure dominants, and it is only by further breeding that their true nature can be ascertained. At the time of Mendel nothing was known about the behaviour of chromosomes, but the modern explanation of what have been called **Mendelian ratios** is based on the chromosome structure of the gametes and the zygotes.

A plant or animal which carries but one set of factors, such as the pure dominant or pure recessive, is said to be **homozygous**, whilst one carrying two sets of factors, such as the impure dominant, or hybrid, is **heterozygous**. The example given, where but two contrasting characters are involved, is an example of **mono-hybridism**, which has been repeated on a large number of plants and animals with similar results.

Occasionally it is found that dominance is incomplete, as in the interesting example of the blue Andalusian fowl. This bird can exist only in the heterozygous condition, and its true homozygous parents are either black, or white with black splashes. When a

blue hen is mated with a similar cock, the offspring
 con blue Andalusians and 25 per cent of each of
 the bl d-white forms, which agree with the propor-
 tions of the F_2 genera When the
 black fowl is mated
 are blue Andalusians.

This can be summarised thus :

	<i>Black</i>	<i>Splashed White</i>		
<i>F1</i>	<i>Blue Andalusian</i>			
	<i>Bl.</i>	<i>BA.</i>	<i>BA.</i>	<i>S.W.</i>

In addition to monohybrid experiments Mendel carried out *dihybrid* experiments, in which he selected *double allelomorphs*, or parents which exhibited two pairs of contrasting characters. For example, he took a garden pea with round yellow seeds, and crossed it with one having angular, or wrinkled green seeds. As in the first experiment, the F_1 generation was found to resemble one parent, all the plants producing round yellow seeds. When the flowers of the plants, formed from these seeds, were self-pollinated, four kinds of seeds were obtained, viz. round yellow, round green, angular yellow, angular green, in the proportions, respectively, 9 : 3 : 3 : 1. The explanation, in this case, is similar to that for a monohybrid cross. The factors dominant are those for roundness and yellow colour, and the unit characters of a pair of allelomorphs will segregate in the gametes. Therefore a gamete will carry one factor for colour and one for shape. The zygote formed in the original cross will contain all four factors, but two of these, viz. for greenness and angular seed, are suppressed or recessive. The gametes of the hybrid can be of four kinds, viz. RY, RG, AY, AG, and both male and female gametes will behave in the same way. The zygotes, formed on self-pollinating the flowers of this generation, can have sixteen different compositions, and it will depend on the factors present in each as to what form the seed displays. The probable behaviour of the gametes of the F_2 generation of a dihybrid cross are shown in Fig. 204, from which it will be realised that the proportions of the types obtained experimentally agree with the probable pairing of the various gametes.

The hybridising of parents possessing more than two pairs of contrasting characters has been carried out since Mendel's time,

and although the results are complicated, it may be said that they can be predicted on the basis of the simpler experiments.

It will be appreciated that interbreeding can cause a reassortment of factors, and the new combinations which may arise when the parents have a complicated chromosome structure are likely to result in the institution of new varieties.

In conclusion it may be mentioned that it has been found possible to induce, artificially, certain of the gene mutations which are known

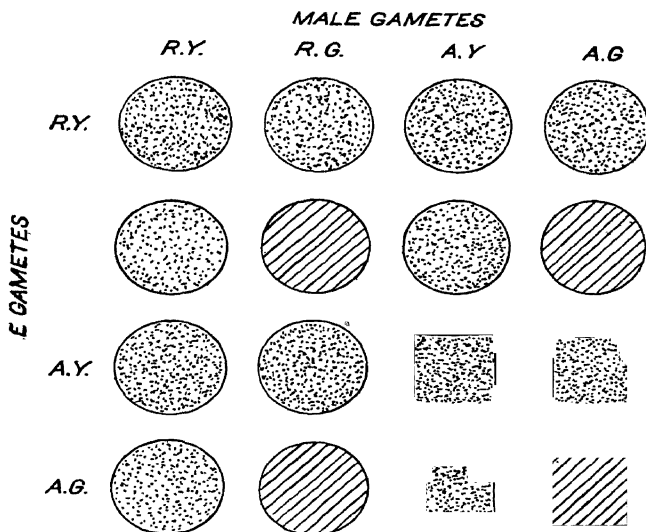


FIG. 204.—Diagram to illustrate the offspring resulting from the self-fertilisation of a dihybrid, obtained by crossing parents with round, yellow seeds and angular, green seeds respectively.

The zygotes produced are shown—yellowness being indicated by a dotted field, and greenness by a shaded field.

In this example, roundness and yellowness are the *dominant* characters, angularity and greenness being *recessive*.

to occur naturally. The fruit fly, *Drosophila*, was subjected to X-rays, which resulted in the production of mutations by either an alteration of the genes within the chromosomes, or an alteration, or *transmutation*, of the chromosomes. In the latter, pieces of chromosomes, with their contained genes, were caused to break away or become associated with other chromosomes, so that in subsequent nuclear divisions, particularly those resulting in sexual cells, new arrangements of the genes became possible. In this way new individuals, breeding true, could become established.

Similar experiments have been carried out on other animals and plants, and it now appears that the evolution of some species, at least, is due to transmutation under natural conditions.

This raises the hope that by means of further experiments on breeding, and the close study of nuclear structure, many of the existing problems of the mechanism of evolution will be elucidated.

APPENDIX

ABRIDGED CLASSIFICATION

I. Plant Kingdom

A. *Cryptogams* (Flowerless Plants)

Phylum.¹ THALLOPHYTA—simple plants without vascular tissues.

Class. ALGÆ—possess chlorophyll, e.g. *Chlamydomonas*, *Fucus*.

Class. FUNGI—devoid of chlorophyll, e.g. *Mucor*, *Psalliota*.

Phylum. BRYOPHYTA. Non-vascular land plants, with an alternation of generations. Female organ, an archegonium.

Class. HEPATICÆ (Liverworts).

Class. MUSCI (Mosses).

Phylum. PTERIDOPHYTA. Vascular land plants with an alternation of generations. Female organ, an archegonium.

Class. FILICALES, e.g. *Dryopteris*.

Class. EQUISETALES (*Horsetails*).

Class. LYCOPODIALES, e.g. *Selaginella*.

B. *Phanerogams*

Phylum. SPERMATOPHYTA—vascular land plants which reproduce themselves by seeds.

Class. GYMNOSPERMÆ—seeds borne nakedly on carpel, e.g. *Pinus*.

Class. ANGIOSPERMÆ—seeds enclosed by carpel.

Sub-class. DICOTYLEDONS, e.g. *Ranunculaceæ*.

Sub-class. MONOCOTYLEDONS, e.g. *Liliaceæ*.

II. Animal Kingdom

(N.B.—Certain phyla are omitted.)

Phylum. PROTOZOA—microscopic unicellular (non-cellular) animals.

Class. RHIZOPODA—locomotion by pseudopodia.

Order. LOBOSA—naked protoplast, e.g. *Amœba*.

Class. MASTIGOPHORA—locomotion by flagella, e.g. *Trypanosoma* (the causal organism of Sleeping Sickness).

¹ The term is used here for the sake of uniformity. A phylum is a division constructed on true relationships. In the plant kingdom, the relationships of associated forms are not always clear, so that some authorities prefer to use the term Division.

- Class. INFUSORIA—locomotion by cilia.
 Order. CILIATA, e.g. *Paramecium*.
- Class. SPOROZOA—internal parasites without organs of locomotion, e.g. *Plasmodium*, *Monocystis*.
- Phylum. CŒLENTERATA—diploblastic animals with radial symmetry. Body-cavity, a cœlenteron, e.g. *Hydra*, *Obelia*, Jelly-fish.
- Phylum. PLATYHELMINTHES—‘Flat-worms.’ Triploblastic animals with bilateral symmetry. No cœlom. No blood system.
- Class. TREMATODA, e.g. *Fasciola*.
- Class. CESTODA, e.g. *Tænia* (Tape-worm).
- Phylum. ANNELIDA. Triploblastic animals with bilateral symmetry. Metamerically segmented. Well-defined cœlom. Alimentary tract with mouth and anus. Closed vascular system. Excretion by nephridia. Central nervous system with ventral nerve cord.
- Class. CHÆTOPODA—locomotion by chætæ, e.g. *Lumbricus*.
- Phylum. ARTHROPODA. Bilaterally symmetrical segmented body. Advanced cephalisation. Jointed appendages. Chitinous exoskeleton. Blood space (*hæmocœle*) surrounds the digestive tract. Ventral nerve-cord.
- Class. CRUSTACEA—highly calcified exoskeleton. Normally, each segment bears a pair of appendages, e.g. *Astacus* (Crayfish).
- Class. ARACHNIDA. Head and thorax fused (= *cephalothorax*), 4 pairs of walking legs, e.g. *Epeira* (Spider).
- Class. INSECTA (Hexapoda). Body subdivided into head, thorax and abdomen. Thorax with 3 pairs of walking legs, and the wings, when present, e.g. *Periplaneta*, *Blatta* (Cockroaches), *Culex*, *Anopheles* (Mosquitoes), *Apis* (Bee).
- Phylum. CHORDATA. Bilaterally symmetrical and highly organised body. Notochord present at some stage of development. Central nervous system with hollow dorsal nerve cord.
- Sub-phylum. CRANIATA (= VERTEBRATA). Notochord replaced by skull and backbone. Highly-developed endoskeleton. Well-defined cœlom. Brain divided into fore, mid and hind parts. Advanced circulatory system, including portal vessels.
- Class. PISCES (Fishes). Dermal scales. Respiration by gills. Fins. Poikilothermic.
- Class. AMPHIBIA. Larval stage aquatic, and respire by gills. Adult amphibious, with pentadactyl limbs. Skin naked. Poikilothermic.
- Order. ANURA, e.g. *Rana* (Frog).

- Class. REPTILIA. Dermal scales, or horny epidermis. Eggs with shell. Embryo with allantois and amnion. Poikilothermic, e.g. Snakes, Crocodile.
- Class. AVES (Birds). Feathers on most of body, legs with dermal scales. Fore-limbs modified to wings. No teeth. Eggs with shell. Embryo with allantois and amnion. Homoiothermic.
- Class. MAMMALIA. Hairy skin. Young born alive (except PROTOTHERIA, which are oviparous). Mammary glands for feeding young. Homoiothermic.
- Order. EUTHERIA, e.g. *Lepus* (rabbit), *Homo* (man).

NOTE.—With the exception of the Protozoa, the above animal phyla constitute the *Metazoa*, or multicellular animals.

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